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PREDATORY BEHAVIOR OF SOME SHORE FISHES IN THE GULF OF CALIFORNIA

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By Edmund S. Hobson

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ABSTRACT

Predatory behavior in some Gulf of California shore fishes was studied to define certain general activity patterns.

Between 1962 and 1965 over 1,200 hours of underwater observations were made at all hours of day and night. Predatory activity in 46 species was observed, and supplemental data were obtained on many others. Digestive-tract contents from 716 specimens were analyzed.

Species that form large, relatively inactive schools close to shore during the day are *Harengula thrissina*, *Selar crumenophthalmus*, *Caranx marginatus* (juvenile), *Selene brevoorti*, *Haemulon sexfasciatum*, *Anisotremus interruptus*, *Microlepidotus inornatus*, *Lythrulon flaviguttatum*, *Orthostoechus maculicauda*, *Xenichthys xanati*, *Lutjanus argentiventris*, *Umbrina xanti*, and *Mulloidichthys dentatus*. All feed nocturnally on prey becoming available after dark. Some species feed in the vicinity of the diurnal schooling sites, but most migrate varying distances offshore. Schools of the sort these fishes form during the day generally are incompatible with their nocturnal feeding, and usually are abandoned after dark in favor of loosely spaced aggregations or independent activity.

Most larger inshore piscivores including *Elops affinis*, *Mycteroperca rosacea*, *Caranx hippos caninus*, and *Nematistius pectoralis*, are primarily crepuscular predators on the diurnally schooling fishes. Predation by *M. rosacea* on *Harengula thrissina* illustrates the intimately related behavior of predator and prey.

Schooling by many prey species reduces the threat of predation. Schooling by some predators facilitates the capture of prey.

All the nocturnally active fishes are predators. Those feeding close to rocky bottom at night, aside from some of the diurnally schooling fishes, are mostly small solitary predators that feed largely on crustaceans. These include *Holocentrus suborbitalis*, *Alphestes multiguttatus*, *Rypticus bicolor*, and *Pareques viola*. Other nocturnal fishes variably aggregate in midwater above the rocks where they prey largely on minute crustaceans. Included are *Myripristis leiognathus* and *Apogon retrosella*. These fishes are relatively inactive under cover during the day.

Feeding habits among the diurnally active fishes are more varied than among those foraging at night.

Most of the diurnal piscivores stalk their prey, as does *Fistularia petimba*, or rush out from cover, as does *Epinephelus labriformis*. Many with these habits are also variably active at night, when at least one, *E. labriformis*, preys largely on crustaceans.

Among diurnal species that prey mostly on invertebrates, those taking plankton in midwater, including *Chromis atrilobata*, *Abudefduf troschelii*, and *Hemipteronotus mundiceps*, aggregate when away from cover. Other diurnal fishes swim close to the bottom, and feed mostly on benthic organisms. A number of these, including various species of Labridae, Pomacentridae, Chaetodontidae and Balistidae, possess morphological and behavioral adaptations that aid in the capture of concealed prey, many of which are nocturnally active invertebrates that seek cover in daylight. The variable utilization of algae as food, and "cleaning" habits are widespread among these groups. Several other small diurnal predators attack from resting positions on the bottom; these frequently stalk or rush out to capture prey, mostly small crustaceans, and include species of Clinidae, Chaenopsidae and Gobiidae. At least most of these diurnal predators are relatively inactive after dark, finding shelter among the rocks or under the sand.

Specialized feeding activity occurs in other diurnal predators, including *Runula azalea*, *Gnathanodon speciosus*, aand *Taenioconger* sp.

Other predators, like *Gymnothorax castaneus*, prey heavily on injured or distressed prey.

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PREDATORY BEHAVIOR OF SOME SHORE FISHES IN THE GULF OF CALIFORNIA

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Studying animals in their natural surrounding provides insight into animal behavior. One can observe interactions among individuals and species not possible when isolated organisms are considered. Close observation of a complex of coexisting, interrelated organsims provides information useful for good design of specialized studies.

So I have attempted to determine some of the factors influencing predatory behavior in marine shore fishes. My data are drawn from direct observations, and I have attempted to describe the activity in such a way that many features of morphology, coloration, and behavior may be better understood. In this effort I have raised more questions than I have answered. But significant progress has been made when intelligent questions can be asked.

There have been few studies of predatory behavior in fishes based on observations of activity in nature. My earlier paper on diurnal-nocturnal activity in fishes (Hobson, 1965a) was a preliminary presentation of many topics considered in this report. Similarly, Starck and Davis (1966), also using direct observations, considered similar questions in a paper dealing with topics presently under study by Starck in the Florida Keys. Among early works are the pioneering observations of William Longley at Tortugas, Fla. More recently, Limbaugh (1955) made a significant contribution with his underwater study of California's kelp-bed fishes. The bulk of information available has been largely from indirect methods. Hiatt and Strasburg (1960), for example, based their extensive study of coral-reef fishes in the Marshall Islands on stomach contents, whereas Suyehiro (1942) presented a comprehensive treatment of fishes in Japan centered around the morphology of the feeding apparatus. Most accounts of predatory behavior in nature are scattered, usually as isolated notes or a few sentences or paragraphs in a larger work. That so few direct observations have been made is readily understandable because only in recent years have technological advances, notably the development of diving equipment, provided us with the means of sustained observations underwater.

I used an experimental approach during an earlier field investigation of shark behavior in the Marshall Islands (Hobson, 1963a). Among other advantages, an experimental program is expeditious. Yet the manipulations of the environment associated with conducting the experiments excluded the possibility of observing behavior under truly natural conditions, even though the work was carried out en-

tirely in the shark's natural habitat. Consequently, in the present program I made no attempt to influence the animals or their environment, but made a strong effort to minimize the effect of my presence on the fishes. From the outset, I attempted to allow activity in the animals themselves to determine the working schedule.

Man is a diurnal creature, and in his biological fieldwork this has been especially evident in studies of habits in marine fishes. Efforts have been concentrated between the hours of 0900 and 1500, which, unfortunately, see a minimum of activity among predaceous species. It was, of course, not possible for me to completely assume crepuscular and nocturnal habits for the duration of my study, but the extent to which I reoriented my efforts in this direction influenced the results. Obviously many workers would find it impossible to commit themselves to such a program, as it is rather exclusive of other activities. Yet with any other method presently available, I believe that not only would many critical questions lie unanswered, but also many critical questions would remain unrecognized.

I should like to acknowledge the numerous suggestions offered by Dr. Boyd W. Walker of the University of California, Los Angeles, during the course of the investigation and preparation of the manuscript. The able assistance of those who assisted in various aspects of the diving operations in Bahia de Palmas, especially Mr. Robert Kiwala and Mr. Gil Powell, is greatly appreciated. I wish to express my appreciation to Adm. Antonio Vazquez del Mercado, Director General of Mexican Fisheries, through whom permission was obtained to carry out the work in Mexican waters. Col. Eugene Walters graciously made available his facilities at Rancho Buena Vista. An early phase of the study was aided by a Sigma Xi-RESA grant in aid of research. I am grateful to Drs. George A. Bartholomew, Jr., Henry J. Thompson, and Vladimir Walters, of the University of California, Los Angeles, and Drs. Carl L. Hubbs and Richard H. Rosenblatt, of Scripps Institution of Oceanography, for their constructive criticism of the manuscript. Finally, I cannot overlook my wife, Karen, who remained remarkably cheerful through it all.

THE STUDY AREA

The program was carried out in Bahia de Palmas, a wide bay on the coast of Baja California Sur, Mexico, in the Gulf of California (fig. 1). My study area within the bay extended along approximately 18 km. of shoreline, mostly a sand beach, from Punta Pescadero south to Punta Soledad (fig. 2).

The bottom over most of the bay is sandy from the beach out to deep water, but there are many isolated areas of rocks that extend from the shoreline out for varying distances offshore. Most of these rocky areas are quite limited in size, but others extend along the water's edge for over 2 km., and out from the beach for 200 m. or more, to where the water is 10 to 15 m. deep. In many areas, a sandy bottom slopes off gradually for about 1 km. or more beyond the outer edge of the rocks before dropping abruptly to greater depths.

The stretches of featureless, open sand that surrounded the rocky areas represent the most extensive inshore habitat in the bay. In several locations submarine canyons cut in through this expanse of shallow bottom almost to the beach. At these points water depths exceeding 30 m. occur within 100 m. of the shoreline, and Shepard (1964) reported depths exceeding 500 m. within 3 km.

My activity centered around the rocky areas. These occur in some locations, for example at Buena Vista, as concentrations of isolated rocks that range in size from

FIGURE 1.—The Cabo San Lucas area of Baja California Sur, Mexico (adapted from photograph, courtesy NASA).

small cobble to large boulders rising more than 4 m. above the bottom. Patches of sand lie among the rocks. In other areas, including Punta Pescadero, massive rock ridges rise sharply from the bottom, sometimes breaking the surface of the water from depths to 12 m. Crevices, caves, and overhangs in these rocks provide cover for many organisms. The rocks support a thick growth of benthic algae, but because the plants are quite small the substrate superficially appears barren. A few areas, Punta Pescadero in particular, support relatively rich populations of coral and gorgonians. Coral reefs were reported in the Gulf of California by Steinbeck and Ricketts (1941), who regarded the area off Cabo Pulmo, which lies about 30 km. south of the study area, as a true fringing reef. However, as Squires (1959) pointed out, these "reefs" are not reefs in the customary physiographic sense, but rather are coral communities. He noted that no appreciable material of bulk is being contributed to the accummulating sediments by the coral community.

Over 300 species of shore fishes occur in the vicinity of the study area (Boyd W. Walker, personal communication). Most of these are representatives of the Panamic fauna to the south. However, a number of western Pacific species and several northern forms are present, in addition to a few endemics. Walker (1960) discussed the affinities of fishes in the Gulf of California.

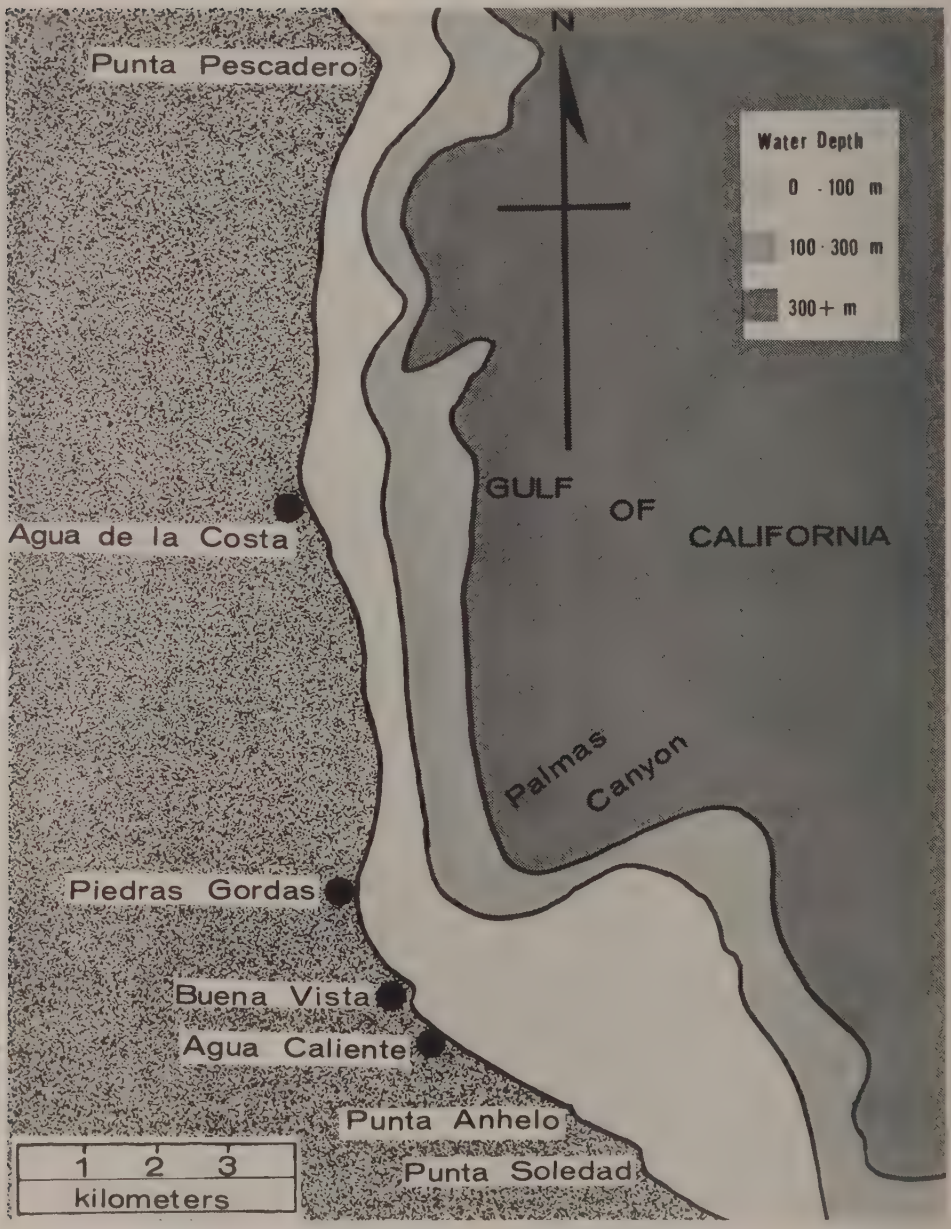

FIGURE 2.—The study area in Bahia de Palmas (adapted from U.S. Hydrographic Office Chart 1664 and Shepard 1964).

Of the species studied, only among the carangids did I note a consistent pattern of seasonal movements: several species present in large numbers during the greater part of the year are generally absent during late winter and early spring. Fluctuations in relative abundance and irregular occurrences were evident in other species, especially in the herring (*Harengula*), but my observations, supplemented by conversations with local fishermen, are insufficient to determine the nature of these fluctuations.

Observations were concentrated during seasons favorable for this work. From April until late August the weather is consistently mild, and no time during this period was lost because of inclement conditions. September and early October are frequently beset by heavy rains, resulting in terrestrial runoff that sharply restricts underwater visibility inshore. Most of my effective work at this time was done out of water. Conditions were favorable from mid-October until late December, when strong winds increasingly limited operations. I did not work in the area from January to March, when extended periods of strong wind generally create unfavorable conditions.

Water temperatures during the study ranged from a low of 20° C. in early April to a high of 31° C. in late August. During the warm months sudden drops in water temperatures often followed extended windy periods. A drop of 3° to 4° C. from one day to the next was not uncommon. On one occasion, during late June, with a strong wind blowing steadily from the southeast, inshore surface temperatures at Buena Vista dropped from 29.4° C. to 21.1° C. in 24 hours.

METHODS

Observations were made over four periods: July to December 1962, July to August 1963, April to July 1964, and October to December 1965. Observations, involving over 1,200 hours under water, were conducted at all hours of day and night. Techniques and problems associated with the diving operations (scuba and snorkeling) were discussed in my earlier report (Hobson, 1965a).

The observations were supplemented by examination of digestive tract contents in 716 specimens collected for this purpose. Most of these fish were examined for both stomach and intestinal contents. All specimens were taken with spear or, with some of the small individuals, "slurp gun" (a collecting device utilizing suction to draw small fishes into a holding chamber). Specimens were usually examined within 15 minutes of their capture.

Invertebrates in digestive tract contents were generally identified only to class, e.g. crustaceans, gastropods, ophiuroids, etc., and some only to phylum, e.g. annelids. Fishes in the diet were identified to species where possible. My aim was to obtain information on the general characteristics of prey in the diet of the various fishes. Where possible, I noted whether a prey item was planktonic or benthic, and if benthic, whether from a sandy or a rocky substrate.

The use of spear and slurp gun offers distinct advantages in colecting specimens for food-habit study. The investigator is able to select particular individuals at certain times of the day and to take specimens from among fish engaged in a particular type of activity. He can also record the activity engaged in by the animal, as well as its surroundings, when taken. Many piscivores regurgitate their food when under stress, and with most collecting methods the regurgitated material may well go undetected, but when a fish is collected by spear or slurp gun regurgitated material can be spotted immediately. I carried a small fine-meshed hand net with me when collecting specimens in order to retrieve such material.

When a large sample of fishes is involved, and prey are relatively small organisms of a uniform size, one can usually estimate the time involved in digestion. This is done through associating observed behavior with condition and position of the ingested material in the digestive tract. Habits that are largely diurnal or nocturnal can usually be recognized readily through observations of activity, supplemented by examination of digestive tract contents from specimens taken during early morning and late afternoon. But in some of the larger predators the apparent digestion time is not readily recognized when prey vary in size, and when feeding times are irregular.

The relative time spent in observing each species is indicated in two ways. "Direct observation" refers to the observations dealing specifically with activity in a particular species. Most such observation involved interactions between two or more individuals. If more than one species was involved, the time was recorded as direct observations for each. "General observation" refers to time spent in the habitat of a species known to be present, even though that species was not directly involved in the observations. This second entry is based on the fact that, with experience in a particular area, one develops a feeling for the "normal situation," so that unusual occurrences are quickly noted, even when attention is focused elsewhere.

Following most periods of direct observations, I made a general survey of the area. Rather than observing particular activity at this time, I remained alert for any activity that seemed to be out of the ordinary. The relative infrequency of unusual behavior added to my confidence in the positive information I had accumulated, largely through direct observations. Negative evidence is difficult to quantify, but during this study substantially contributed to the development of my ideas. Obviously my figures for general observations are rough estimates, particularly for species that occur irregularly, as do most large, free-swimming predators.

Although observations were made through all months of the year except January, February, and March, it was not possible to work with each species throughout this period. I concentrated on different phases of the study when conditions were favorable for that particular work. Nevertheless, during the course of the program I incidentally noted seasonal changes in behavior and relative abundance in some species. Although I made no special effort to gather this material, a considerable amount of general information on seasonality accumulated and is introduced into the report where pertinent.

In referring to species in this report as nocturnal, diurnal, or crepuscular, I have subscribed to an artificial classification that presents an oversimplified picture. Designations are based on the period during which most feeding occurs. Sources of variation from this scheme are undoubtedly many and complex. At present, little is known in this area of study. Certainly moonlight profoundly affects nocturnal activity, as will be discussed in reference to many of the species treated in this report. The placement of several species, as will be noted, is quite arbitrary, based on my data.

All references in this report to the length of fishes are to Standard Length.

TERMINOLOGY

Schools vs. aggregations

Variability in social groupings of fishes resists a rigid classification scheme, and the terms "school" and "aggregation" have carried different meanings for different authors. I will not attempt to review this literature. Distinctions made in the different reports usually reflect aspects of be-

havior being emphasized by the authors, and disagreements are often largely semantic. I feel that present knowledge does not permit a satisfactory nomenclature.

I have drawn functional distinctions between two types of associations, because I feel that these distinctions are important in the general ideas I develop. Associations among the fishes I studied were one or the other type, depending on the nature of the activity in which the fishes were engaged. I refer to one type as an aggregation, and to the other type as a school. My use of these terms is meant only to aid in presenting the material; I do not suggest that such usage necessarily applies to other situations.

As fishes considered here are all particulate feeders, taking their prey one by one, feeding groups present a characteristic appearance. The spacing between individuals, while variable, is relatively great, and as each of the members orients on discrete pray organisms they all tend to face in different directions. There is a marked degree of independent activity in these fishes. I refer to such groups as aggregations.

On the other hand, nonfeeding individuals often form groups in which members are relatively close together and uniformly spaced in comparison with members of aggregations. All face in the same direction when in motion, but in stationary groups orientation between members is often highly variable. Such stationary groups generally show little sign of activity. There is little evidence of independent activity in these fishes, with members tending toward synchronized behavior. I refer to these associations as schools.

Under this usage, one must regard with caution any concept of an "aggregating species" as opposed to a "schooling species." Most fishes considered here will adopt either type of association, depending on circumstances. Thus the nocturnally active pomadasyids are described as forming schools during the day, but as dispersing at night in favor of feeding aggregations and independent activity. On the other hand, some diurnally active fishes school when not actually feeding, but then break away from their school when food becomes available. For example, the loose, active schools in which the small jack *Caranx caballus* swims during the day are abandoned in a flurry of activity when feeding begins, but immediately reform when feeding ceases. Thus these fish shift from school to aggregation then back to school again, all in rapid succession. Magnuson and Prescott (1966) described disruption of schooling with the introduction of food in the Pacific bonito *Sarda chiliensis*.

Many small diurnal predators feeding on plankton in midwater, such as *Chromis atrilobata*, are active in aggregations, but immediately discontinue feeding and school when threatened by a predator. At such times they switch from an aggregrate of feeding individuals to a synchronized, alerted formation.

Sunrise and sunset

I use times calculated for longitude and latitude of Bahia de Palmas as provided by the Nautical Almanac (U.S. Naval Observatory). Sunrise, thus calculated, approximates the time the sun actually appears above the Gulf of California. The sun sets behind the mountains approximately 20 to 30 minutes before time of sunset as used here.

It was not practical to use observed times of sunrise and sunset. Cloud cover, particularly over the mountains, and the fact that I was frequently underwater at these times, necessitated using the tables.

OBSERVATIONS

The observations are presented by species, grouped in families, and according to nocturnal, diurnal, or crepuscular feeding habits.

NOCTURNAL SPECIES

CLUPEIDAE

Harengula thrissina (Jordan and Gilbert): Flatiron herring (fig. 3)

Estimated period of direct observations: 94 hours.

Estimated period of general observations: 100 hours.

During daylight throughout most of the fall months, 1962, flatiron herring schooled in vast numbers at various points along the shoreline. A far lesser, but still considerable, number were present during the late spring months of 1964, although I understand from local fishermen that herring are frequently very abundant in the spring. At least some herring seemed to be present throughout the year, with the possible exception of late winter and early spring.

Schools along the shoreline, with members mostly 60 to 100 mm. long, always form over rocky bottom right at the water's edge. They generally remain at a particular location for periods of up to several weeks. Frequently, the herring appear in a location shortly after a school has left another spot several kilometers away, suggesting that just one school is involved. When present, these small fish are heavily preyed on by a wide variety of predators.

Flatiron herring are relatively inactive

FIGURE 3.—*Harengula thrissina* schooling inshore.

during the day, remaining essentially stationary and quiet in dense schools from before dawn until after sunset. Many hours of observations indicate that these fish do not feed diurnally, and that no individuals become separated from the schools in daylight. Except when attacked by predators, a relatively infrequent occurrence during most of the day, these fish do little more than hover over the rocks.

Around sunset the herring become increasingly active, as do a wide variety of predators that begin to increase in numbers around the school at this time. With growing darkness and predation, segments of the herring school make abortive forays a short distance away from the beach, only to return quickly to the main school—often under pressure from predators. About 20 minutes after sunset the entire school goes into motion, and starts moving away from shore. Usually the school follows a path that keeps it over rocky bottom for as great a distance as possible away from the beach. On some occasions, predation abruptly ceases about the time the school starts offshore, whereas at other times flurries of predation become intense at various points in the outward migration. These topics are dealt with below when discussing activity in predators that exploit these schools. Data on the timing of the offshore migration are also presented below.

Conclusions regarding nocturnal activities of the herring are limited, because observations involved only a few scattered individuals and relatively small, loosely spaced groups that I encountered in midwater over the sand offshore. The herring apparently feed on plankton, which abounds at night. Since vast numbers of these fish move away from the beach shortly after sunset, perhaps most of them move out beyond the area where I worked at night. Their progress offshore may be readily observed from shore through the activity of feeding pelicans that accompany them over 400 m. beyond the outer edge of the rocks. About there, diving activity in these birds gradually slackens and they return to shore. All evidence of predation by fishes has disappeared from the surface of the water by this time as well. Whether this general decrease in observed predatory activity reflects dispersal of the school, or the rapidly fading daylight, I do not know. In my attempts to follow the herring schools away from the beach in the evening, I always lost contact with them in the growing darkness before noting any sign of their dispersing or altering their course. Lavenburg and Fitch (1966) took large numbers of *H. thrissina* around midnight in surface tows over 40 to 75 m. of water near Agua Verde Bay, which is about 160 km. to the north of Buena Vista in the Gulf of California.

Observations made at Buena Vista during November 1962 provide the following picture of activities at dawn. At first light, about 1 hour before sunrise, herring appear near the surface over sandy bottom, close to the outer edge of the rocky area. The number of herring, as well as the tightness of the school, gradually increases until about 30 minutes before sunrise. Then the school, having reached daytime proportions, moves in over the rocks to its shallow-water diurnal schooling site.

Although I did not collect herring for food-habit study, I did examine stomach contents of specimens at the University of California, Los Angeles, collected by B. W. Walker. All nine specimens, 85 to 107 mm. long, collected with an ichthyocide at Cabo San Lucas, 3 hours after sunrise, were full of what seemed to be largely a single species of small shrimplike crustacean. On the other hand, all 10 specimens, 75 to 108 mm. long, taken at 1630 in a beach seine near Guaymas were empty. These data agree with the view that these fish feed during the night while they are offshore, probably taking at least a major portion of their food from the plankton.

Herring less than about 50 mm. long show behavior distinct from that outlined above. The following is based on observations made during the fall of 1962, when the larger herring were most numerous along the beaches. At such times the smaller individuals do not join the larger herring inshore, but instead are scattered about in small schools near the surface 50 m. and more offshore. A few of these small fish occasionally appear with the larger individuals next to the beach, but only in distinct subschools that form above or on the periphery of the main school. During the summer months of 1963 and 1964, few larger herring were seen, but the small herring were periodically abundant. It became evident that the small herring usually do not remain in any one area over successive days, as the larger individuals generally do, but rather seem to be constantly in motion near the surface over depths in excess of 5 to 6 m., 50 m. and more offshore.

In general, my incidental observations on small herring indicate that the schools are usually quite small, less than about 2 m. in diameter, and are frequently accompanied by small to medium-sized predators, approximately 100 to 300 mm. long, that swim below the school and occasionally burst into a flurry of activity. In one location about 100 m. offshore from Punta Anhelo, a large flat reef lies in 8 to 10 m. of water. This reef, with an area of about 25 by 50 m., does not rise more than 1 or 2 m. above the surrounding bottom and is faced on all sides by an expanse of open sand. During much of August, 1963 and 1964, a large stationary school of herring, with members approximately 30 to 40 mm. long, hovered each day high in the water column over this reef. Serranids and carangids, some over 600 mm. long, were generally in the vicinity of this school at all hours of the day, and ocasionally engaged in brief flurries of predation.

Conclusion

The flatiron herring is a nocturnal predator that moves offshore to feed largely on plankton at night. Individuals over about 50 mm. long are inactive in large dense schools next to the beach during the day; individuals less than about 50 mm. long usually swim in smaller schools near the surface farther offshore.

LITERATURE ON OTHER CLUPEIDAE

Starck and Davis (1966) reported only nocturnal habits in herring of the Florida Keys; these species feed after dark on plankton after schooling in dense numbers during the day. Included here are *Harengula pensacolae*, *H. humeralis*, *Jenkinsia lamprotaenia*, *J. majua*, and *Sardinella anchovia*. They described schools of *Jenkinsia* breaking up into smaller, more loosely associated feeding groups at night.

Suyehiro (1942) found that *Harengula zunasi* feeds on diatoms and copepods from the plankton, whereas Hiatt and Strasburg (1960) noted that *Harengula kunzei* in the Marshall Islands feeds on the shallow bottom fauna, mostly crustaceans.

MURAENIDAE

Gymnothorax castaneus (Jordan and Gilbert): Pacific green moray (fig. 4)

Estimated period of direct observations: 31 hours.

Estimated period of general observations: 700 hours.

This large, solitary predator, often over 1200 mm. long, was present on all inshore rocky areas during the entire program. Members of this species are frequently active in the open during the day, usually swimming close to the rocks, but occasionally moving over open sand 10 to 20 m. from the nearest cover. Yet despite the relative frequency of these excursions, this moray most often lies quietly on the bottom among the rocks during both night and day. Although I speared 11 specimens,

FIGURE 4.—*Gymnothorax castaneus* during a diurnal foray.

941 to 1169 mm. long, between the hours of 0700 and 1730, none contained food, except one that had just eaten a fish that had escaped from me after being speared.

Fishes taken for stomach content analysis occasionally tore themselves from the spear and found shelter beneath the rocks. On a number of such occasions these morays sensed the wounded fish from distances exceeding 20 m., and swam to the rock for the capture. None of the other predators indicated they were aware of, or interested in, these wounded fish. In the Marshall Islands I have seen some sharks, for example *Carcharhinus* spp. respond to this situation in a similar manner (Hobson, 1963a), but to my knowledge no sharks were in the area during the observations referred to here.

Prey need not be injured to elicit an attack by a moray; this is illustrated by the following account, quoted from my field notes:

> . . . as I swam close to the bottom, a large scorpionfish *Scorpaena mystes*, which had been lying unseen on a rock before me, darted from my path and alighted on a patch of sand next to a rock. Almost instantly a large moray *G. castaneus* shot out from under a rock and grasped the scorpionfish from the side, just behind the head. The scorpionfish, which was positioned crossways between the moray's jaws, did not struggle. In fact, is showed no sign of distress whatsoever, but simply rested quietly in the moray's grasp. The moray, on the other hand, was unable to swallow this large prey as it was situated between its jaws. Neither fish moved for at least 10 to 15 seconds. Finally the moray momentarily relaxed its grasp—probably in order to shift the prey around in its mouth for swallowing. However, the instant the moray released its hold, the scorpionfish darted away like a shot.

On two occasions, upon grasping a spiny lobster, *Panulirus* sp., at the base of its antennae, and attempting to wrest it from a rocky crevice, I found myself engaged in a tug of war with a large *G. castaneus* that had established a firm hold with its jaws on the lobster's tail.

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Predation by *G. castaneus* is not limited to chance encounters with prey in some form of distress. At dusk one evening during July 1964, I witnessed a situation that emphasized the flexibility in feeding habits of fishes. At the surface, over 3 m. of water, a large *G. castaneus*, approximately 1 m. long, was thrashing about, snapping vigorously at members of a large school of larval fishes, each of which was no more than 10 mm. long. This attack on larval fishes was probably an exceptional incident. I cannot believe the moray was successful in this effort, although I have no data on this point. In any event, the incident illustrates the potential variability in predatory behavior, even where an animal appears to be highly specialized—perhaps expressed here after an extended period without food.

Conclusion

This moray is an opportunistic predator, highly responsive to stimuli emanating from a fish in distress or engaged in some form of unnatural behavior. It probably takes such individuals whenever they become available, day or night.

LITERATURE ON OTHER MURAENIDAE

Gosline and Brock (1960) remarked that the stomachs of morays collected in Hawaii are usually empty. Hiatt and Strasburg (1960) attributed a high incidence of empty stomachs among species of *Gymnothorax* in the Marshall Islands to nocturnal habits. However, considering the size of prey taken by large morays, some evidence of nocturnal feeding should be evident in a large sample collected during the day, especially if specimens are taken in the morning. I believe the lack of food in stomachs of large morays in these collections may reflect infrequent feeding, rather than nocturnal feeding, even in situations where the animal might obtain most of its food after dark. Morays are generally reported to be nocturnal (Winn and Bardach, 1959; Starck and Davis, 1966).

OPHICHTHIDAE

Myrichthys tigrinus Girard: Tiger snake eel

Estimated period of direct observations: 2 hours.
Estimated period of general observations: 100+ hours.

I observed snake eels only infrequently, but considering the numbers that often appear in poison stations, lack of observations is probably due largely to their being under the sand most of the time. I have no reason to believe they were not present in the area during the entire study.

I encountered *M. tigrinus* on a number of occasions when solitary members of this species, ranging up to approximately 500 mm. long, undulated on the sand. They were observed during both day and night, among rocks as well as over open sandy bottom. I did not effectively observe their behavior at night, but in daylight they move over the bottom with their tubelike nostrils close to the sand. Periodically they pause, then thrust their heads into the sand with a vigorous effort in which that part of the body still protruding thrashes vigorously. I did not examine stomach contents, but on several occasions was able to identify the quarry as small crabs through body parts protruding from the eel's jaws after its head emerged from the sand. Although entering the sand head first after prey, they seek cover when threatened by entering tail first. I do not know whether they feed when buried, or if they occupy subsurface burrows. I did not observe this eel away from the bottom during my observations underwater, but from a boat saw it appear at the water's surface under a night light on several occasions where water depth exceeded 20 m.

Conclusion

This snake eel usually burrows, but occasionally emerges onto the surface of the sand. It feeds on small animals buried in the sand, such as crustaceans, which it probably takes with equal facility day or night. It may find nocturnal crustaceans on the surface of the sand at night readily available. Placement of this eel among the nocturnal species is quite arbitrary on the basis of my data.

LITERATURE ON OTHER OPHICHTHIDAE

In the Florida Keys, Starck and Davis (1966) observed the larger ophichthids, including *Myrichthys oculatus*, with greatest frequency at night, and suspected that they feed nocturnally. On the other hand, they felt that a lack of sightings of other, smaller species, known to be in the sand, indicated that they feed on the interstitial fauna and seldom emerge from the substrate.

Hiatt and Strasburg (1960) remarked that the two species of ophichthids they studied in the Marshall Islands do not live in permanent burrows, but rather burrow in the sand. Noting that the eyes of *Brachysomophis sauropsis* are near the tip of its snout, they suggest that this eel "lies under the sand with just the tip of its snout protruding, keeping watch for prey inadvertently crawling or swimming close to it."

HOLOCENTRIDAE

Holocentrus suborbitalis (Gill): Pacific squirrelfish

Estimated period of direct observations: 2 hours.
Estimated period of general observations: 600 hours.

As the last daylight fades in the evening, squirrelfish of this species emerge from the rocky crevices that shelter them during the day, and scatter individually about among the rocks. They occur on all the rocky areas along the shore, and were present during the entire study. Staying close to the bottom, this predator is a solitary animal while foraging at night.

With the first trace of morning light, they return to their rocky shelters. Five individuals, 88 to 110 mm. long, taken within 3 hours of sunrise had fed on crustaceans. During the day they remain under cover and as nearly as I could tell do not feed during this period. I noted nocturnal activity of *H. suborbitalis* in my earlier report (Hobson, 1965a).

Conclusion: This squirrelfish is a nocturnal predator, feeding largely on small crustaceans. It remains sheltered under rocky cover during the day, but emerges to feed solitarily at night close to the bottom. No evidence of diurnal feeding was obtained.

Myripristis leiognathus Valenciennes: Pacific soldierfish

Estimated period of direct observations: 14 hours.
Estimated period of general observations: 700 hours.

Soldierfish of this species are active at night over rocky areas throughout the bay, where they were present during the entire study period. Some are dispersed among the rocks, but most aggregate in midwater. They are particulate feeders on plankton, that is, they take each plankter individually in a manner indicating that the capture is visually directed.

On dark nights the aggregations venture farther above the rocks, and are more dispersed, than during moonlight. When threatened, the members draw close together and dive toward rocky cover below. The color of *M. leiognathus* is solid red when the fish is under cover during the day, but when it is active in the open after dark its ventral surface is silvery, thus providing a countershading effect. When held in the beam of a diving light this nocturnal pattern is lost, and the solid red diurnal coloration returns.

At first light in the morning these fish return to their rocky retreats, and thus are not in open water during twilight or daylight. Eleven specimens, 65 to 95 mm. long, were taken from rock crevices between one hour before and one hour after sunrise. All had fed on a large variety of tiny crustaceans, including many crab larvae. Three had also fed on small fishes, and one contained sand and a gastropod mollusk as evidence of at least some benthic foraging. Throughout the day they remain under the shelter of the rocks. That they do not take food at this time is evidenced by the empty stomachs of all 16 specimens, 78 to 102 mm. long, taken with spear and slurp gun from these same crevices during the afternoon. I noted nocturnal activity of *M. occidentalis* (= *M. leiognathus*) in my earlier report (Hobson, 1965a).

Conclusion

This predator feeds nocturnally on small crustaceans and some fishes, largely from the plankton; to a lesser extent on the benthos. It tends to form aggregations when active away from cover, but is solitary when foraging on the bottom. There is no evidence that it feeds while sheltered under rocks during the day.

LITERATURE ON OTHER HOLOCENTRIDAE

Nocturnal habits in holocentrids are well established. For example, Longley and Hildebrand (1941) described nocturnal habits in *Holocentrus* at Tortugas, Fla. Hiatt and Strasburg (1960) remarked that *Myripristis* and *Holocentrus* are nocturnal in the Marshall Islands, and Starck and Schroeder (1966) reported the same to be true at Alligator Reef in the Florida Keys.

Al=Hussaini (1947) reported that *Holocentrus sammara* and *H. diadema* in the Red Sea feed wholly on crustaceans. He suggested that the red coloration of these fishes, which is characteristic of holocentrids in general, may be related to pigments obtained from their crustacean diet.

SERRANIDAE

Alphestes multiguttatus (Günther): Pacific guaseta

Estimated time of direct observations: 4 hours.

Estimated time of general observations: 700 hours.

A relatively small serranid, attaining a maximum length of about 250 mm., this predator was present on all the inshore rocky areas during the entire study. Members of this species have secretive diurnal habits, frequently concealing themselves in algae or rocks or even lying on their sides under a thin layor of sand. Little if any food is taken during the day, as evidenced by the empty stomachs of all 10 specimens, 96 to 165 mm. long, speared during the afternoon.

These predators emerge from their diurnal cover during evening twilight to begin nocturnal foraging. After an active night close to the bottom among the rocks, they return to cover during morning twilight. Seven specimens, 89 to 172 mm. long, were speared within 1 hour after sunrise. The stomachs and intestines of six were full of food in all stages of digestion, and though the stomach of the seventh was empty, its intestine was full. Prey were mostly benthic crustaceans, although one of these serranids had ingested a small octopus, and another a small fish.

Conclusion

This nocturnal predator feeds mostly on benthic crustaceans close to the bottom among the rocks. It is inactive during the day, when cover is sought among rocks or algae or under the sand.

Epinephelus labriformis (Jenyns): Flag cabrilla (fig. 5)

Estimated period of direct observations: 8 hours.
Estimated period of general observations: 700 hours.

This medium-sized predator, which generally does not exceed a length of 375 mm. as an adult, was numerous on all inshore rocky areas during the entire study period. Although members of this species frequently swim over the bottom, close to rocks or coral, they usually rest motionless on the bottom with their heads facing out from partial cover. From this position, and throughout the day, they rush forward to capture prey that have ventured near. Twenty-five specimens, 95 to 340 mm. long, were speared between noon and sunset. Of the 12 containing food, 7 (58 percent) had fed exclusively upon small fishes, while the other prey were largely crustaceans. The prey fish were small animals active among the rocks, like pomacentrids and blennies.

While most of the predators I am considering have feeding habits that clearly are predominantly diurnal, nocturnal, or crepuscular, *Epinephelus labriformis* seems to feed actively at all hours of day and night. Nevertheless, foraging appears to be the more productive after dark, even though I did not directly observe them feeding at night.

Thirteen of the fourteen individuals taken with empty stomachs were among the 25 specimens speared during the afternoon, and the other one was captured at 1130. With this lone exception, all 34 specimens, 112 to 241 mm. long, taken during the morning had food in their stomachs. Furthermore, there is evidence that

FIGURE 5.—*Epinephelus labriformis*, a solitary predator.

the diet of this species differs between day and night. Seventeen individuals were speared between 1 hour before sunrise and not more than 30 minutes after sunrise. Some of these contained freshly ingested prey that had probably been captured during morning twilight. In addition to this material, however, all contained at least moderately digested material that had undoubtedly been ingested during previous night. Only one of these contained fish remains exclusively whereas another contained fish remains and crustacean fragments. The other 15 (88 percent) had fed exclusively on crustaceans, a striking contrast to the strictly piscivorous diet in 58 percent of those which had food in their stomachs during the afternoon.

Conclusion

This predator feeds regularly during both day and night, although its nocturnal foraging appears to be the more productive. Prey taken at night are mostly small crustaceans, while diurnal prey are mostly small fishes that are captured with a rush from cover. All prey are captured on or near the bottom.

LITERATURE ON OTHER SERRANIDAE

Relatively extensive foraging during both day and night, as occurs in *E. labriformis*, apparently is also found in other members of the genus. Longley (1916) reported that *Epinephelus morio* at Tortugas fed indifferently by day or night. Starck and Davis (1966) remarked that species of *Epinephelus* in the Florida Keys behave in a similar manner day and night, referring specifically to *Epinephelus striatus*. They also noted probable crepuscular peaks in feeding by these species, but I could not definitely establish this in *E. labriformis*.

GRAMMISTIDAE

[Until recently, the soapfishes were included among the serranidae]

Rypticus bicolor (Valenciennes): Pacific soapfish

Estimated period of direct observations: 4 hours.

Estimated period of general observations: 700 hours.

The largest individuals of this relatively small species are approximately 250 mm. long. They occurred on all the inshore rocky areas during the entire study, but observations were limited owing to their secretive diurnal habits. During the day most of them remain concealed among the rocks. Nevertheless, some prey are captured at this time, for although four of five specimens, 78 to 204 mm. long, collected during the afternoon had empty digestive tracts, the fifth contained four recently ingested shrimps.

During evening twilight these soapfish emerge from cover to begin a nightlong period of foraging close to the bottom among the rocks. Of four specimens, 115 to 203 mm. long, speared between 1800 and 2000, the digestive tracts of two were empty, but the other two both contained small freshly ingested benthic crabs. All four specimens, 195 to 248 mm. long, taken after 2000 and before first light in the morning, contained prey in varying stages of digestion; three had fed on crustaceans while the fourth had captured a small fish. These predators return to their diurnal retreats during morning twilight. I remarked earlier (Hobson, 1965a) that *R. bicolor* is a nocturnal predator.

Conclusion

This soapfish is a solitary nocturnal predator, feeding mostly on benthic crustaceans near the bottom among the rocks. It remains relatively inactive during the day under rocky cover.

LITERATURE ON OTHER GRAMMISTIDAE

Starck and Davis (1966) reported nocturnal habits in three species of *Rypticus* in the Florida Keys.

APOGONIDAE

Apogon retrosella (Gill): Cortez cardinalfish

Estimated period of direct observation: 11 hours.

Estimated period of general observations: 620 hours.

During the day this cardinalfish schools beneath rocks, or in the shadow of overhanging ledges. It occurs on all the rocky areas in the bay, and was present during the entire program.

All five specimens, 57 to 77 mm. long, taken with spear and slurp gun during late afternoon had empty stomachs. Only five of 13 individuals, 45 to 90 mm. long, taken during early afternoon had empty stomachs. Yet, although the remaining eight contained the remains of small crustaceans and a few small fishes, all this material had undergone extensive digestion. There was no good evidence that this species does much feeding during the day.

After last light in the evening, these fish emerge from cover. Some scatter over the rocks, whereas others rise into midwater where they form aggregations and are particulate feeders on plankton. Sometimes, but by no means always, *A. retrosella* loses much of its red color and becomes quite pale when in midwater at night. On dark nights they rise considerably higher into the water column and are considerably more dispersed than during moonlight. On nights of bright moonlight they remain in relatively tight aggregations and do not venture far from the rocks. When threatened, these fish draw close together and dive toward the sheltering rocks.

At first light in the morning they return to their diurnal shelter, and thus are not in the open during the twilight periods or during the day.

Conclusion

This cardinalfish feeds nocturnally, largely on small crustaceans and some fishes. It emerges into the open to feed at night, after being sheltered under rocks during the day. Much of its prey is taken from the plankton in midwater, where it tends to form aggregations when active away from cover. It is solitary when feeding on benthic organisms.

LITERATURE ON OTHER APOGONIDAE

Hiatt and Strasburg (1960) suspected nocturnal habits in *Gymnapogon philippinus* of the Marshall Islands because of its secretive diurnal habits, but reported that other apogonids in that area are diurnal. Longley and Hildebrand (1941) noted the secretiveness of *Apogon maculatus* during the day, and its emergence at dusk, but expressed uncertainty regarding its nocturnal habits. Randall (1963) noted nocturnal habits in a Virgin Island apogonid, and Starck and Davis (1966) stated that all seven apogonids in the Florida Keys are nocturnal. Starck and Davis found only one of these, *Apogon conklini*, to feed on plankton, remarking that this species forages in midwater "individually or in groups." They also remarked that several of these diurnally red cardinal fishes fade to a pale hue at night. Al=Hussaini (1947) noted that *Apogon auritus* in the Red Sea feeds exclusively on crustaceans and suggested that the red coloration of this species, and many other apogonids, may be related to pigments obtained from a crustacean diet.

CARANGIDAE

Selar crumenophthalmus (Bloch): Bigeye scad

Estimated period of direct observations: 52 hours.
Estimated period of general observations: 272 hours.

A large school of bigeye scad, composed of individuals approximately 175 to 225 mm. long, was present at Buena Vista throughout the day during most of the study, but I rarely saw members of this species elsewhere in the bay. The school at Buena Vista is generally positioned about 20 m. from the beach over rather open bottom that is largely covered with dark algal scum. An extensive concentration of rocks lies nearby, and isolated large rocks are scattered throughout the schooling area. Most of the time schools of two pomadasyids, *Lythrulon flaviguttatum* and *Microlepidotus inornatus*, are nearby during daylight.

Scad seem to be absent from this region during early spring. In 1964 they first reappeared during mid-April. The early arrivals were in small groups of six to twelve individuals that swam rapidly along the beach at the water's edge. As their numbers increased, they moved offshore and formed a subschool within the larger school of *M. inornatus*. The scad did not disassociate themselves from the school of grunt until mid-May, when, their numbers having increased considerably, they formed a large, relatively inactive school of their own.

I did not observe scad separated from this school as long as it was present. In addition, I saw no evidence that members of the school engage in any diurnal feeding.

As with the nearby pomadasyids, large predators keep the diurnal school under surveillance much of the time, and periodically attack it during the day. Predation is particularly severe during the twilight periods.

The scad become increasingly active as daylight fades, finally moving offshore about 20 minutes after sunset. I was not able to follow these rapidly swimming little fish as they moved away from the beach in the growing darkness, and I did not encounter them while working at night. Furthermore, I did not witness their reappearance inshore in the morning, although they are present in their large school at the regular diurnal locations as early as 20 to 30 minutes before sunrise. Ten specimens, 185 to 209 mm. long, speared from schools during midday, all contained the well-digested remains of fishes. One individual also contained crustacean fragments, and three had ingested sand and debris. This material, through fragmentary, all points toward largely piscivorous nocturnal feeding offshore.

My failure to observe *Selar crumenophthalmus* at night may have reflected nocturnal habits that take members of this species out over deeper water. Lavenberg and Fitch (1966) took a single specimen at night in a surface tow over 75 to 85 m. of water 2 km. off Ceralvo Island in the Gulf of California.

Susumu Kato, of the U.S. Bureau of Commerical Fisheries (personal communication), reports catching large numbers of bigeye scad, using a jig at night near Cabo San Lucas. He took them close to shore, both near the surface and close to the bottom. Perhaps signficantly, very deep water occurs close to shore in that area. Yamaguchi (1960) reported that *S. crumenophthalmus* is taken by handlines in Hawaii at night. Hiatt and Strasburg (1960) found *S. crumenophthalmus* forming large schools in protected waters of the lagoon at Arno Atoll in the Marshall Islands where juveniles reportedly feed largely on benthonic sand dwelling organisms. I observed a large school of these scad

during the day near shore in the lagoon at Eniwetok, Atoll, also in the Marshall Islands. This school was consistently in the same location during the day over a 3-month period, swimming in a dense, relatively inactive congregation that frequently milled in the same manner as did the school at Buena Vista. Longley and Hildebrand (1941) reported that *S. crumenophthalmus* schools near shore in the Tortugas, Florida, where one specimen contained a small fish and a shrimp.

Conclusion

This nocturnal predator moves offshore at night to feed largely on fishes. Some crustaceans also are taken. It remains relatively inactive in schools near shore during the day.

Caranx marginatus Gill: Pacific horse-eye jack

Estimated period of direct observations: 2 hours.

Estimated period of general observations: 96 hours.

Although I observed only juveniles of this jack in Bahia de Palmas, these were present in some areas, particularly at Piedras Gordas and Buena Vista, throughout the period of the study. They occur in two size groups, each showing distinctive behavior. Individuals less than approximately 200 mm. long swim in schools over rocks in very shallow water along the beach. These fish have prominent vertical bars on their sides. Individuals more than approximately 200 mm. long lose the vertical bars and become a plain dark grey dorsally and lighter ventrally, and develop light tips on the longer leading rays of dorsal and anal fins. These larger fish are located during the day up to 200 m. away from the beach, where they form dense inactive schools in 6 to 8 m. of water over rocks or over adjacent sandy bottom. The largest individuals I found were less than 300 mm. long. I did not see any larger members of this species, despite the fact that individuals exceeding 600 mm. long are common in some other areas.

I observed no evidence of diurnal feeding. Nine specimens, 170 to 215 mm. long, speared from schools during the late afternoon, were without food in their stomachs or intestines. I did not observe them move offshore in the evening, but they were not present in their diurnal schooling locations after dark.

Although I cannot be certain that I have observed juveniles of *C. marginatus* at night, on a number of occasions, all under moonlight, I encountered active groups of small jacks, 200 to 300 mm. long, along the outer edge of rocky areas. These may well have been *C. marginatus*, but under these conditions of decreased visibility I could not distinguish them from the morphologically similar *C. hippos caninus*. Nevertheless, whereas *C. marginatus* of this size are numerous in the area, *C. hippos caninus* of this small size are not. I did not observe the return of these small predators to shallow water in the morning, but they are present in schools at their diurnal locations before surise. Three specimens, 204 to 290 mm. long, collected within 2 hours after sunrise from the diurnal schools, all had full stomachs and intestines. Prey in the diet of all three included crustaceans and well-digested herringlike fishes. Three additional specimens, all 210 mm. long, taken from schools during midday, contained only crustacean fragments in their stomachs, although their intestines were full of crustacean fragments and unidentifiable material.

Although I did not observe adult *Caranx marginatus*, Susumu Kato (personal communication) reports taking many individuals exceeding 600 mm. long with hook and line after dark in the Revilla Gigedo Islands, Mexico, where they are called "night jacks."

Conclusion

This jack is a nocturnal predator. The juveniles feed on small midwater fishes and crustaceans after dark, remaining relatively inactive in schools close to shore during the day.

Selene brevoorti (Gill): Mexican lookdown

Estimated period of direct observations: 9 hours.
Estimated period of general observations: 95 hours.

Lookdowns in the bay seemed to be confined to a single school, composed of adults approximately 300 to 400 mm. long, located in the Buena Vista area. I observed this school repeatedly, but irregularly, during the study. Usually these fish swim over relatively open sandy bottom, perhaps 30 to 50 m. beyond the schooling site of *Selar crumenophthalmus*, in an area that I visited infrequently. Occasionally they appear along the outer edge of the rocks offshore from Buena Vista point. Water depth in both areas is about 6 to 8 m.

I did not see any lookdowns separated from the school during the day. All seven specimens, 318 to 356 mm. long, that I took from the school during midafternoon were without food in their digestive tracts, suggesting that they had not engaged in any diurnal feeding.

I did not observe these fish during evening twilight, but after dark encountered a few solitary individuals close to the bottom over the open sand offshore. I was unable to find them in their regular diurnal school area at night.

Although I was never present in the diurnal schooling area during morning twilight, I made a number of visits to this area within the 2 hours immediately following sunrise, and at these times speared 13 specimens, 305 to 360 mm. long, for food habit study. The four of these that had food in their stomachs all contained the well-digested remains of fishes. The lone prey fish that was in any way identifiable was recorded simply as "herringlike." Stomachs of the other eight lookdowns were empty, but seven of these had food in their intestines: five contained fish remains, and two held crustacean fragments. The digestive tract of one individual taken shortly after sunrise was empty. This material suggests predominantly nocturnal piscivorous habits.

Conclusion

The lookdown is a nocturnal predator, feeding to at least a large extent on small midwater fishes over the open sand offshore. It remains relatively inactive in schools during the day.

LUTJANIDAE

Lutjanus argentiventris (Peters): Yellow pargo

Estimated period of direct observations: 15 hours.
Estimated period of general observations: 550 hours.

According to my observations, this snapper consistently occurs over inshore rocky areas of the bay during daylight, usually in variably sized schools that are spread out close to the bottom near the outer edge of the rocks. At any time of the day, however, a considerable number of these fish move among the rocks, individually or in small schools. Individuals over approximately 400 mm. long are generally solitary, retiring to caves during daylight. Of nine active members of this species, 200 to 446 mm. long, speared among the rocks during the afternoon, the stomachs of four were empty, although their intestines contained the broken shells of mollusks and crusacean fragments, one stomach contained fish bones, another a single crab claw, and two individuals taken during midafternoon were full of recently ingested herring. Thus at least some feeding is diurnal.

In the evening, the diurnal schools do not disperse abruptly or move in well-defined patterns. Rather, they simply become increasingly active around sunset and gradually disperse among the rocks during twilight.

Throughout the night these fish are scattered among the rocks, often moving into very shallow water near the beach where, with the pomadasyid *Anisotremus interruptus*, they are often the largest fish present. I did not see any members of this species over the open sandy areas at night.

The larger schools begin to form with first light in areas where they are located during the day. Four specimens, 254 to 335 mm. long, taken within 3 hours after sunrise, all had full stomachs. Food ingested included crabs, shrimps, mollusks, and one small fish. A comparison of this material with the incidence of empty stomachs among specimens taken later in the day is suggestive of predominantly nocturnal feeding habits. I noted that feeding habits of *L. argentiventris* were primarily nocturnal in my earlier report (Hobson, 1965a).

Conclusion

This nocturnal predator also feeds appreciably by day. At least most prey are taken on or near the bottom from among the rocks. Prey consist largely of crustaceans, but other invertebrates, as well as fishes, are also taken. Most of these snappers are relatively inactive in variably sized schools during the day.

LITERATURE ON OTHER LUTJANIDAE

Lutjanids are widely recognized as having nocturnal feeding habits. Longley (1916, 1917) reported nocturnal foraging by snappers at Tortugas. His conclusions are based largely on a comparison of stomach contents from specimens taken early in the morning with other material taken from specimens collected late in the afternoon. Breder and Halpern (1946), examining stomach contents of a tropical Atlantic snapper, *Lutjanus griseus*, reported that one group of these predators regularly traveled over half a mile between their diurnal schooling area and their nocturnal feeding ground. Randall and Brock (1960) concluded from stomach-content analysis that *Lutjanus vaigiensis* in Tahiti forage primarily at night, although at least some diurnal feeding was indicated by the presence of some fresh food in their stomachs during the day. Starck and Davis (1966) noted that the lutjanids of the Florida Keys are primarily nocturnal, but feed to a varying extent diurnally. At least one member of the family, the plankton-feeding *Ocyurus chrysurus* of the tropical Atlantic, reportedly feeds as actively during the day as it does at night (Longley, 1916). But Starck and Davis (1966) remarked that commercial hook-and-line fishermen are most successful fishing for this snapper after dark.

POMADASYIDAE

Haemulon sexfasciatum Gill: Greybar grunt (fig. 6)

Estimated period of direct observations: 103 hours.

Estimated period of general observations: 700 hours.

During the day, large schools of *H. sexfasciatum* hover along the outer edge of the rocky areas. The fish constituting these large schools, all approximately 250 to 375 mm. long, generally show no sign of feeding, but a few individuals at the base of the schools occasionally nose about in the sand, presumably for food. The stomachs of all seven specimens, 245 to 310 mm. long, taken from the schools during midafternoon were empty, indicating that the members of these schools had engaged in little if any feeding. However, a few diurnally active members of this species move slowly among the rocks, either as individuals or in small groups, hovering much of the time

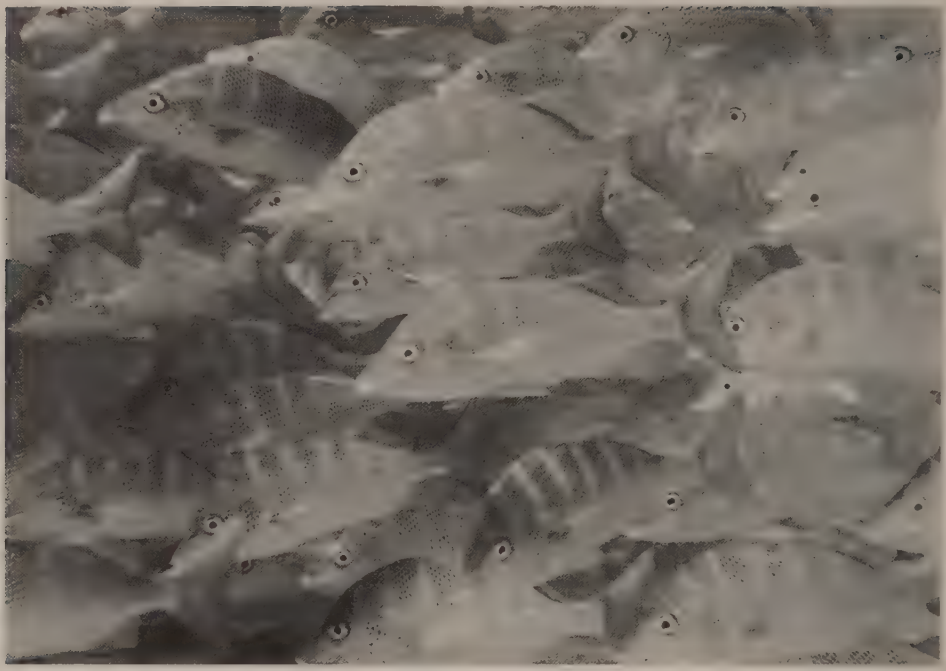

FIGURE 6.—A school of *Haemulon sexfasciatum*.

close to the sand, intently regarding a spot on the bottom before them. I observed one such fish dart forward from its hovering position, jab its snout into the sand, and with a vigorous movement in which its head twisted sharply upwards it pulled out an annelid at least 150 mm. long. The barred color pattern in this fish, which is evident at all times, becomes particularly intense when this fish feeds during the day. Of the five diurnally foraging individuals, 267 to 380 mm. long, that were speared during midafternoon, one had an empty stomach and the other four all contained recently ingested annelids.

The large schools disperse during the late period of evening twilight. No migration is involved, and the dispersal itself is not abrupt; the members gradually move away a few at a time. Most of these fish move in among the rocks; a lesser number swim out over the open sand. I noticed no period of intense predation on members of this species during twilight.

When these fish feed nocturnally, the barred color pattern becomes particularly intense, just as it does in those feeding during the day. Three solitary members of the species, 270 to 290 mm. long, speared as they moved among the rocks between 2300 and 0100 all contained freshly captured annelids. One also had ingested two small chitons.

The schools gradually reform in their regular diurnal locations during the period shortly after first light. All 11 specimens, 256 to 320 mm. long, taken from recently reformed schools within 1 hour after sunrise had full stomachs. This observation, when compared with that of empty stomachs of specimens taken from these schools during the afternoon, provides strong evidence for predominantly nocturnal feeding habits. Food in this species is composed

entirely of benthic animals, including lancelets, ophichthid eels, benthic crustaceans, pelecypods, chitons, and annelids. The juveniles form small schools in shallow water near the beach. During the late period of evening twilight, when several other pomadasyids migrate offshore, small schools of these little fish also swim away from the beach. But they usually disperse among the rocks before traveling more than about 30 m.

Conclusion

Haemulon sexfasciatum is a nocturnal predator that engages in appreciable diurnal feeding. Most individuals are inactive during the day in large schools. All prey is taken from the bottom; at least many of the prey are fossorial. Most individuals forage among the rocks, but some feed over the open sandy areas.

Anisotremus interruptus (Gill): Burrito grunt

Estimated period of direct observations: 23 hours.

Estimated period of general observations: 600 hours.

The variably sized schools of *A. interruptus* usually spread out close to the bottom, mostly along the outer edge of the rocky areas during the day. Individuals longer than 400 mm. tend toward solitary habits, and usually rest close to rocky cover during the day.

This species displays notably more diurnal activity than do other pomadasyids in the bay. Nevertheless, stomach contents of nine specimens, 240 to 410 mm. long, taken while they moved in small groups among the rocks during midday, did not indicate extensive diurnal feeding. Although the intestines of all were full of a wide variety of benthic organisms, only two had material in their stomachs. These two contained benthic crustaceans, mollusk shells, sand, algae, and debris.

The diurnal schools of these fish, as those of *Haemulon sexfasciatum*, show neither a well-defined evening migration nor an abrupt dispersal. During the later stages of twilight the schools break up as the members become increasingly active and gradually disperse among the rocks.

During the night these grunts are scattered over the rocky area, often moving right in to the water's edge, where, with the snapper *Lutjanus argentiventris*, they are often the largest fish present. I did not see any individuals of this species over the open sandy areas offshore at night.

The large schools begin to form with first light in the areas where they are located during the day. All eight specimens, 249 to 345 mm. long, taken from the schools within 3 hours after sunrise had full stomachs. Food items included anemones, soft corals, annelids, mollusks, crustaceans, and small fishes. This finding, along with that of empty stomachs in specimens taken at a later hour, strongly suggests predominantly nocturnal feeding habits.

Conclusion

Anisotremus interruptus is a nocturnal predator, which also engages appreciably in diurnal feeding. A wide variety of prey, mostly invertebrates, is taken from the bottom among the rocks. Most individuals are relatively inactive in variably sized schools during the day.

Microlepidotus inornatus Gill: Wavy-line grunt (fig. 7)

Estimated period of direct observations: 64 hours.

Estimated period of general observations: 300 hours.

Large diurnal schools formed by this species are densely packed, and frequently fill the water column from surface to bottom in 2 to 6 m. of water. A school composed of individuals 200 to 300 mm. long is consistently present at Buena Vista, but the species is only infrequently seen else-

FIGURE 7.—A school of *Microlepidotus inornatus*.

where in the bay. The school at Buena Vista is generally located in the same relatively open area described above as the schooling site of *Selar crumenophthalmus*. Occasionally, the school moves over the nearby rocks, but diurnal movements are largely limited to sluggish shifts in position over the relatively open area.

I did not observe these grunts feeding during the day, and rarely encountered them away from the large school. The few exceptions, all solitary individuals, occurred in areas where the schools were not present, for example at Punta Anhelo. These were always very timid individuals that seemed to be cowering in the shadows of overhanging rocks or other cover, their fins and gill covers beating rapidly. Other than such behavioral signs of stress, these fish often showed physical evidence of ill health, such as frayed fins and blemishes on their bodies.

Members of the school at Buena Vista are often heavily preyed on by large piscivores, particularly during the twilight periods. This predation reaches a peak approximately 20 minutes after sunset, then ceases abruptly. Within minutes thereafter the school moves offshore and disperses over the open sand. The offshore migration occurs at approximately the same time each evening, even when no predators are present.

These were among the fishes I encountered most frequently over the open sandy expanses after dark—some as individuals but most in loosely spaced groups within a few meters of the bottom. During moonlight the groups are more tightly spaced than on darker nights.

With first light, the school at Buena Vista begins to reform near the outer edge of the rocks. Both the size and density of the school continues to increase for about 20 minutes. Then, having reached diurnal proportions about 30 minutes before sun-

rise, the school moves in over the rocks to assume its daytime position near the beach.

All 10 specimens, 204 to 280 mm. long, collected within 2 hours after sunrise from these recently reformed schools were full of prey, whereas all seven, 204 to 283 mm. long, taken late in the afternoon were empty. Exclusively nocturnal feeding is strongly indicated. Seven specimens were full of what appeared to be mostly a single species of midwater shrimplike crustacean, whereas 10 specimens were full of benthic material, almost all of which seemed to be of a single species of pelecypod mollusk. This mollusk was tentatively identified as *Transennella putella*, which Keen (1958) reported to live "mostly offshore in depths to 45 fathoms." A few benthic crustaceans were mixed with this material. Only one individual contained both benthic and midwater organisms, and these were sharply separated within the digestive tract.

Conclusion

Microlepidotus inornatus is strictly a nocturnal predator that moves offshore at night to feed on both midwater and benthic invertebrates over open sand, not among rocks. Members of a school may feed largely on a single species of prey during a given feeding period. This grunt is inactive during the day, congregating in large, dense schools near shore.

Lythrulon flaviguttatum (Gill): Cortez grunt

Estimated period of direct observations: 58 hours.

Estimated period of general observations: 250 hours.

A large, densely packed school of these fish, all adults 200 to 300 mm. long, is consistently present at Buena Vista during the day, but I did not see this grunt schooling elsewhere in the bay. The school at Buena Vista is located immediately adjacent to the school of *M. inornatus*. The two groups, which are of similar size, merge to varying degrees, and generally remain together during occasional sluggish shifts in position.

As is also true for *M. inornatus*, the only members of this species encountered away from the large schools during the day were solitary fish showing clear signs of stress. These were occasionally found sheltered among the rocks in areas where the schools were not present.

This grunt is exploited in the same manner, at the same time, and by the same predators as is *M. inornatus*. Furthermore, *L. flaviguttatum* also migrates offshore shortly after the large piscivores have withdrawn, and then disperses over the open sand. The offshore migration of this species also occurs at about the same time in the evening, even when no predators have been in the area. I encountered this fish in loosely spaced groups over the sand after dark, but not as frequently as I did *M. inornatus*, perhaps because *L. flaviguttatum* generally seems to operate at higher levels in the water column. This pomadasyid also seems considerably more dispersed on dark nights than when there is a bright moon.

I did not observe them reforming their school in the morning, but the school appears intact at the regular diurnal schooling site about the same time as does the school of *M. inornatus*.

The stomachs in 11 of 14 specimens, 250 to 290 mm. long, taken from recently reformed schools within 2 hours of sunrise were full of prey. The other three had empty stomachs, but full intestines. All 12 specimens, 240 to 306 mm. long, taken from these same schools later than 5 hours after sunrise had empty stomachs, and all but one of these also had empty intestines. Exclusively nocturnal feeding is strongly indicated. The fish that I sampled had fed largely on a single species of tiny, midwater, shrimplike crustacean—the same

crustacean as was found in several specimens of *M. inornatus*. Only one of 15 specimens showed any evidence of benthic feeding, this being some crushed mollusk shells in the intestine.

Juveniles of *L. flaviguttatum*, along with the young of the other pomadasyids, school at the water's edge during the day. These small fish occur in large numbers during November and December, when they migrate offshore in the evening at about the same time that the adults move out. Although I experienced difficulty following the adults offshore, I was readily able to maintain contact with the slower swimming juveniles. The nocturnal movements of the younger fish, which are approximately 100 to 150 mm. long, are considerably more restricted than those of the adults. The following account, quoted from my field notes, records observations made one evening during late November 1962, as I accompanied a small school of juvenile *L. flaviguttatum* moving away from the beach at Agua Caliente:

> The small school moved away from the beach, swimming among the rocks, until they encountered the expanse of open sand about 30 yards offshore. Here they stopped and swam about among the rocks at the rock-sand interface. Periodically, small segments of these groups ventured out over the sand, only to be driven back by one or several of a number of machetes (*Elops affinis*) that were patrolling the area. These abortive forays away from the rocks gradually increased in frequency, and included greater numbers of individuals, until finally the whole school streamed out over the sand and dispersed. By this time it was almost dark, and machetes were no longer present. At first the little grunts remained nestled in hollows between the ripples in the sand. Gradually, however, many rose up into midwater until they occupied the entire water column in this area where depth was 10 to 12 feet.

Conclusion

This grunt is strictly a nocturnal predator, moving offshore over open sand at night to forage mostly on midwater invertebrates, but some benthic material is also taken. Members of a school may feed largely on a single species of prey during a given feeding period. They do not feed among the rocks and are inactive during the day in large, dense schools near shore.

Orthostoechus maculicauda Gill: Spottail grunt

Estimated period of direct observations: 2 hours.
Estimated period of general observations: 48 hours.

This species appeared only occasionally at Buena Vista, Punta Soledad, and Agua de la Costa. During the day adults between 200 to 300 mm. long school over rocky bottom in very dense, inactive groups that nearly fill the water column in 3 to 4 m. of water within 20 m. of the beach.

Diurnal movements of these schools are limited to sluggish shifts in position within a limited area. During the day I did not observe these grunts feeding, nor did I encounter individuals away from their large school. Occasionally individuals in these schools swim to the bottom, turn on their sides, and scrape their flanks on the bottom. On several occasions they lined up, awaiting a turn to scrape themselves against a broken mollusk shell. This activity, which may be an attempt to rid themselves of some growth or ectoparasite, is also engaged in by *Microlepidotus inornatus*, and occasionally by *Lythrulon flaviguttatum*.

The school migrates offshore in the evening at about the same time as do the schools of *M. inornatus* and *L. flaviguttatum*. I did not observe intensive predation on *O. maculicauda* just before its migration. In moving offshore, individuals swim out across the

rocks and then continue over the open sand where they disperse. During the night they are frequently active in loosely spaced groups within 3 m. of the bottom. I have no data on the reforming of the school in the morning, nor were stomach contents examined.

Conclusion

This grunt also is strictly a nocturnal predator feeding over open sand offshore. It does not forage among the rocks. During the day it remains inactive in large dense schools inshore.

Xenichthys xanti Gill: Bigeye grunt

Estimated period of direct observations: 4 hours.
Estimated period of general observations: 75 hours.

Throughout most of the study, relatively small schools of these predators, comprised of individuals about 175 mm. long, were present at Buena Vista during the day. They generally remain over sandy bottom in shallow water next to the beach, where water depth does not exceed about 2 m. As I visited this habitat only infrequently, I made relatively few observations of these schools.

I did not observe any fish separated from their schools during the day, nor did I see evidence of diurnal feeding. I have no data on their twilight or nocturnal movements, except that at night they were not present in their regular diurnal locations. But they were present at these locations as early as 20 minutes before sunrise. Seven specimens, 168 to 184 mm. long, speared for stomach-content analysis within 1 hour after sunrise, had full digestive tracts. The diet of five was composed entirely of midwater crustaceans, including many crab larvae; one had fed exclusively on fishes (the one identifiable prey specimen was a clupeid); the seventh had ingested benthic crustaceans as well as a little sand.

312-390 O—68——3

Conclusion

This fish is strictly a nocturnal predator, moving offshore at night to feed largely on small midwater crustaceans, and on some fish and benthic material. It is relatively inactive during the day in schools near shore.

LITERATURE ON OTHER POMADASYIDAE

Pomadasyids are widely recognized as nocturnal feeders. Longley (1916, 1917) reported nocturnal habits in grunts at Tortugas. His conclusions were based primarily on a comparison of stomach contents from specimens collected during early morning with other material taken from specimens collected late in the afternoon. Randall (1963) noted that pomadasyids in the Virgin Islands are nocturnal and also that they generally move away from their diurnal schooling sites to forage at night. Longley and Hildebrand (1941) also remarked that areas away from the reef are important feeding grounds for many members of this family. Starck and Davis (1966), treating the grunts of the Florida Keys, provided information on their movements between diurnal schooling areas and nocturnal feeding grounds. In my earlier report (Hobson, 1965a), I briefly outlined some of the material on Gulf of California pomadasyids that is presented in greater detail in this paper.

MULLIDAE

Mulloidichthys dentatus (Gill): Mexican goatfish

Estimated period of direct observations: 56 hours.
Estimated period of general observations: 700 hours.

Members of this species occur consistently over all the inshore rocky areas in the bay. During the day most individuals longer than about 250 mm. congregate near the outer edge of the rocks and frequently form mixed schools with the pomadasyid

Haemulon sexfasciatum. At the same time, smaller goatfish, along with a few larger individuals, swim in considerable numbers closer to shore. Fish in this latter category tend to move actively among the rocks in a number of relatively small groups, many working their barbels through the sand and amid the short stubble of benthic algae on the rocks. However, such diurnal feeding efforts do not seem to be particularly productive. Of 11 specimens, 135 to 310 mm. long, speared during midday and afternoon from among these small active groups, two contained mollusks and crustaceans, one contained part of a brittlestar arm along with sand and various debris, and the other eight were empty. Relatively few larger goatfish engage in this seemingly unprofitable diurnal activity: most hover quietly in their schools farther offshore. Six specimens, 260 to 310 mm. long, taken from these larger schools during midafternoon were all empty, indicating that they had engaged in little if any diurnal feeding.

These goatfish become increasingly active at dusk and gradually disperse over the rocky area during twilight. Some forage on the surrounding open sand after dark, but most are over the sandy patches among the rocks, where they occur in small, loosely spaced groups or as individuals.

With first light in the morning the goatfish begin to reassemble into larger groups, although most remain active throughout much of the twilight period. By sunrise they have assumed their diurnal positions. Twenty-four specimens, 152 to 285 mm. long, were speared within 2 hours of sunrise from among the larger individuals offshore, as well as from the smaller fish closer to the beach. The stomachs and intestines of 22 were full of prey. Of the remaining two, one had an empty stomach but full intestine, and one was completely empty. Prey consumed included annelids, mollusks, benthic crustaceans, and dactyloscopid fishes. A comparison of these data with material collected later in the day strongly indicates predominantly nocturnal feeding habits.

Conclusion

This goatfish is a nocturnal predator that engages in some diurnal feeding, particularly by smaller individuals. All prey are taken from the bottom and at least many of them are fossorial. Most foraging occurs among the rocks, but some prey are taken from the surrounding open sand. The species remains relatively inactive in schools during the day, but forages solitarily and in small, loosely spaced groups at night.

LITERATURE ON OTHER MULLIDAE

Species of *Mulloidichthys* are widely reported to possess nocturnal habits. Gosline and Brock (1960) noted that *Mulloidichthys auriflamma* in Hawaii feeds after dark, and Longley (1916) reported nocturnal habits in *Mulloidichthys martinicus* at Tortugas, Fla. Longley and Hildebrand (1941) remarked that whereas some members of the species *M. martinicus* forage during the day, these diurnal efforts are largely unproductive, just as I found for *M. dentatus*. Starck and Davis (1966) suspected nocturnal habits in *M. martinicus* in the Florida Keys. They also noted that this goatfish often schools during the day with pomadasyids and lutjanids, thus paralleling my observations of *M. dentatus* frequently schooling with *Haemulon sexfasciatum*.

SCIAENIDAE

Umbrina xanti Gill: Blackmouth croaker

Estimated period of direct observations: 6 hours.

Estimated period of general observation: 35 hours.

This croaker tends to frequent shallow

water over open, sand-pebble bottom near the beach—a habitat I visited only infrequently. Its occurrence in the area is also irregular, contributing to limiting my observations on members of this species. They swim in variably sized schools spread out close to the bottom. I did not see any of them separated from the schools during the day, but members of the schools are quite active, and when they occasionally move among the rocks the schools tend to break up somewhat. I collected five specimens, 225 to 235 mm. long, late in the afternoon. Four of these had empty stomachs and intestines; the fifth had a partially digested crab in its stomach.

I did not observe these fish during evening twilight but after dark frequently saw solitary individuals foraging over the bottom in the same areas frequented by the schools during the day. I did not see them further offshore at night.

Although I did not observe them regrouping in the morning, I collected eight specimens, 220 to 270 mm. long, from schools within 1 hour of sunrise. All had full stomachs and intestines. Of three additional specimens, 228 to 260 mm. long, taken from the schools within 3 hours of sunrise, two had full stomachs and intestines, whereas the third had food only in its intestine. Prey of these croakers includes benthic crustaceans, mostly crabs, as well as mollusks and benthic fishes. Fishes in the diet include species that occur on a sand-pebble bottom, such as *Chaenopsis alepidota* and dactyloscopids.

Conclusion

Umbrina xanti is a nocturnal predator that engages in some diurnal feeding. Prey consists of benthic invertebrates and fishes from open sand-pebble bottom near shore. This species is usually solitary when active at night. During the day it usually remains relatively inactive in schools near shore.

Pareques viola (Gilbert): Rock croaker

Estimated period of direct observations: 11 hours:

Estimated period of general observations: 700 hours.

During the entire study period, this nocturnal croaker was active on all of the inshore rocky areas throughout the night. Solitary fish move about close to the bottom among the rocks. Seven specimens, 115 to 140 mm. long, captured with spear and slurp gun within 1 hour after sunrise had stomachs and intestines full of different crustaceans exclusively.

With daylight, they return to the shelter of caves or shadowy recesses beneath the rocks, where they join others of their species, often forming relatively large concentrations. Little feeding occurs during the day. Of seven specimens, 20 to 153 mm. long, taken with spear and slurp gun during late afternoon, the digestive tracts were empty in all but one, which contained a few crustacean fragments. An additional 160 mm.-specimen collected during midday contained partly digested crustaceans in its stomach. I mentioned the diurnal-nocturnal habits of *P. viola* in my earlier report (Hobson, 1965a).

Conclusion

Pareques viola is a solitary nocturnal predator that feeds largely on small benthic crustaceans among the rocks. It remains inactive under rocky cover during the day, often in concentrations.

LITERATURE ON OTHER SCIAENIDAE

Starck and Davis (1966) reported that *Equetus pulcher* and *Odontoscion dentex* form diurnal groups of as many as 20 individuals in holes in the reef, and range out individually at night to forage over the surrounding bottom. They also reported occasional nocturnal sightings of *Equetus punctatus* in the open on the reef. Longley and Hildebrand (1941) described similar behavior in *Equetus acuminatus* (=*E. pulcher*) at Tortugas.

Diurnal Species

HETEROCONGRIDAE

Taenioconger sp.: Garden eel (fig. 8)

Estimated period of direct observations: 3 hours.
Estimated period of general observations: 42 hours.

This garden eel is an undescribed species (R. H. Rosenblatt, personal communication). The largest individuals I saw were about 900 mm. long. Large numbers are concentrated in various open sandy areas exposed to a strong current, and where water depth exceeds approximately 4 to 6 m. Although observations were infrequent, owing to irregular visits to areas where the eels are abundant, this unique animal seemed to be present throughout the study period.

During the day members of this species keep their tails in their burrows, while extending most of their bodies directly upward from the sand so that their heads are perhaps 40 cm. above the bottom. From this position they face into the current, feeding on minute organisms that drift by. Thus, although they do not leave their burrows, they nevertheless subsist largely on plankton. Their large eyes, as well as the manner in which they reach out to pick food items being carried by the current, indicates that food is located visually. I did not examine stomach contents, but am confident that this animal is a diurnal feeder, obtaining little if any food after dark. They withdraw into their tubes with last light, and although I carefully checked the garden eel beds at all periods of the night, not only had the eels withdrawn from sight but also their tubes were covered over with sand.

FIGURE 8.—Garden eels, *Taenioconger* sp.

Conclusion

This garden eel inhabits tubes in open sandy bottom exposed to a current, where it feeds on planktonic organisms. With tail secure in its tube, its head is extended a considerable distance above the bottom so that it has access to the plankton. It withdraws into its tube at nightfall and remains nocturnally inactive.

LITERATURE ON OTHER HETEROCONGRIDAE

Rosenblatt (1967), among others, remarked on plankton-feeding habits in garden eels, and cited various morphological adaptations to this mode of life. In addition to pointing out that a strongly oblique mouth is often associated with feeding on plankton, he acknowledges W. A. Starck II for noting that the shortened snouts of these fishes permit close-range binocular vision. Rosenblatt also draws attention to the large eyes and reduced cephalic lateral line systems, as well as the reduced olfactory organs, as further evidence of an increased dependence on vision for locating food.

Starck and Davis (1966) did not observe *Nystactichthys halis* at night, and suspected that this plankton-feeding garden eel of the Florida Keys is inactive at that time.

FISTULARIIDAE

Fistularia petimba Lacépède: Pacific cornetfish (fig. 9)

Estimated period of direct observations: 6 hours.

Estimated period of general observations: 500 hours.

During the day this unique predator swims slowy over the rocks, usually less than 1 m. from the substrate. Members of this species were present during all periods of the study—many of them over 1 m. long.

The cornetfish are usually active in

FIGURE 9.—The cornetfish, *Fistularia petimba*, a stalking predator.

loosely spaced groups of a few individuals. They are stalking predators that show no sudden movement until they have gained a position very close to their prey. When properly positioned for the capture, they often draw their midsection into a modified "s" (as viewed from above), and may also momentarily display a series of distinct bars on their bodies. At this point they suddenly dart forward to engulf their prey. This predator often uses the body of another fish, like a grouper or parrotfish, as a shield behind which to approach its prey.

Ten specimens, 535 to 995 mm. long, were speared for study of food habits. A wide variety of small fishes are captured at all hours of the day. Prey include benthic species, such as ophichthid eels, clinids, and trypterygiids; free-swimming fishes that are active close to cover, such as pomacentrids; schooling fishes, such as herring; and even such surface fishes as hemiramphids. Obviously the cornetfish is not limited to minute food organisms, as a casual appraisal of its tubular snout and mouth might suggest. One 880-mm. specimen contained three ophichthid eels each more than 300 mm. long. Hiatt and Strasburg (1960) noted the ability of *Fistularia petimba* to capture relatively large fishes in the Marshall Islands and pointed out that Suyehiro (1942) must have been mistaken when he reported that this species takes only minute planktonic organisms by using its tubular snout as a pipette.

I saw no evidence of nocturnal feeding by this species, although individuals were noted in the same positions at night as during the day.

Conclusion

This predator feeds diurnally on small fishes that are captured after stalking. It often uses other fishes as shields behind which to approach its prey. There is no evidence of nocturnal feeding.

LITERATURE ON OTHER FISTULARIIDAE

Starck and Davis (1966) described activity in *Fistularia tabacaria* from Florida that suggests primarily nocturnal habits. Vladimir Walters, of the University of California (personal communication), has taken *F. tabacaria* with beach seine off the New Jersey coast, but only at night.

Eibl-Eibesfeldt (1955) described the manner in which the trumpetfish *Aulostomus maculatus*, a species related to the fistulariids, uses other fishes as cover behind which to approach its small prey in the Indian Ocean.

CARANGIDAE

Gnathanodon speciosus (Forskål): Toothless jack

Estimated period of direct observations: 6 hours.
Estimated period of general observations: 250 hours.

This is a relatively large jack that sometimes exceeds 1 m. in length. Members of this species were present over the rocky areas during all periods of the study, swimming in schools 1 to 2 m. above the bottom during the day.

Periodically the schools descend to the bottom, for these jacks feed strictly on benthic organisms. In obtaining food they move rapidly from rock to rock, quickly working over the surface of each rock with their highly protrusible, toothless jaws. Occasionally they work through small pockets of debris collected in depressions in the sand. Ten specimens, 215 to 602 mm. long, taken with spear between midmorning and late afternoon were full of a wide variety of small, active benthic animals, including shrimps, crabs, amphipods, mollusks, and small fishes. Judging from the large numbers of benthic animals in their stomachs, along with the absence of sand and detritus, they are obviously effective not only in capturing prey, but in doing so selectively. I detected no effort to

stalk or select individual prey; the manner of feeding in this species has more the appearance of a grazing herbivore than of a predator. This jack was not seen at night.

Young of *G. speciosus* display "piloting" habits. That is, they swim in close association with larger fishes, usually predators. A discussion of this phenomenon, and its possible role in providing the small jacks with a degree of protection from predators, was in an earlier report (Hobson, 1963b).

Conclusion

This diurnal predator feeds on small benthic animals. It does not seem to seek out individual prey, but by use of its highly protrusible, toothless jaws, works through the algal cover on rocks to capture small prey concealed there. No evidence of nocturnal feeding was found.

CHAETODONTIDAE

Heniochus nigrirostris (Gill): Barberfish (fig. 10)

Estimated period of direct observations: 30 hours.
Estimated period of general observations: 700 hours.

As an active "cleaner," this butterflyfish forms variably sized stationary schools in specific locations over rocky bottom during the day. By referring to this species as a "cleaner," I mean that it enters into a symbiotic relation with other fishes wherein it removes, as food, ectoparasites or diseased tissue from the bodies of the other fishes. The subject of cleaning symbiosis in the marine environment was recently reviewed by Feder (1966). Areas where members of this species concentrate are cleaning stations, and the butterflyfish aggregate here to await members of other species that visit these stations to be cleaned. The stations I observed were continuously maintained in the same locations during the entire 3.5-year period of the study.

When a group of fish arrive in the area for cleaning, the butterflyfish disperse from the school and move out to meet them, generally operating as individuals. Although most cleaning occurs close to the bottom, these chaetodontids frequently swim up into midwater, or even to the surface, in order to clean a visitor. I remarked on cleaning habits of *H. nigrirostris* in earlier reports (Hobson, 1965a, 1965b).

In referring to cleaning by *H. nigrirostris* in the Gulf of California, Feder (1966), basing his remarks on observations by Conrad Limbaugh, stated, "The butterflyfish are always paired, and all prominent rocky points are occupied by at least one pair of adults." Apparently he was unaware that cleaning stations maintained by members of this species usually involve a relatively large number of individuals, sometimes over several hundred.

Thirteen specimens, 95 to 165 mm. long, speared for food habit study contained crustaceans, minute gastropods, algae, and fish scales—the latter often with attached bits of flesh.

Although these chaetodontids are specialized as cleaners, and show distinctive behavior that is associated with their cleaning habits, they also feed to a considerable extent on benthic organisms picked from rocky substrate. At such times they are usually active in groups of two or three individuals.

At night they rest quietly near the bottom, often under partial cover. When there is a bright moon some may move about near the rocks, often in groups of two or three. Nevertheless, examination of the digestive tracts from four active individuals, 95 to 130 mm. long, collected between midnight and 0100 when there was a bright moon, showed no signs of recent feeding. At night they display a dark "smudge" on the side and lose the black stripe that runs along the base of the dorsal fin.

FIGURE 10.—A cleaning station maintained by *Heniochus nigrirostris*.

Conclusion

Heniochus nigrirostris is a diurnal omnivore somewhat specialized as a cleaner. It is largely inactive at night.

LITERATURE ON OTHER CHAETODONTIDAE

I remarked on diurnal habits of the herbivorous *Holocanthus passer* in my earlier report (Hobson, 1965a). Starck and Davis (1966) reported similar diurnal activity patterns for all nine species of chaetodontids that they observed in the Florida Keys. Schroeder and Starck (1964) illustrated the nocturnal color of *Chaetodon ocellatus*, which displays a large dark "smudge" on its side at night, similar to that of *H. nigrirostris* after dark.

POMACENTRIDAE

Chromis atrilobata Gill: Castañeta (fig. 11)

Estimated period of direct observations: 8 hours.

Estimated period of general observations: 700 hours.

This damselfish swims in stationary midwater aggregations above the rocks throughout the day, where it is a particulate plankton feeder. Throughout the study period it was found that aggregations occupy the same locations over all the rocky areas of the bay. They rise from the rocks into midwater shortly before sunrise and return to cover just after sunset; they are absent from open water during the later periods of evening twilight, the early periods of morning twilight, and at night. Members of these diurnal midwater feeding aggregations are generally loosely spaced, but when the group is threatened they abruptly discontinue feeding and draw close together. When danger becomes more imminent they dive to the sheltering rocks. A few individuals, dispersed among the rocks, are active near the bottom during the day.

Ten specimens, 98 to 141 mm. long, collected at various times of the day had fed on small crustaceans exclusively. I found no evidence of nocturnal feeding. At night they are scattered among the rocks where they remain quiet but alert.

Conclusion

This damselfish is a diurnal predator, active in midwater aggregations, where individuals feed largely on planktonic crustaceans.

Abudefduf troschelii (Gill): Pacific sergeant-major (fig. 12)

Estimated period of direct observations: 10 hours.

Estimated period of general observations: 780 hours.

Aggregations of *A. troschelii* occur over all of the rocky areas in the bay during the day, where they are particulate plankton feeders. They were present at these locations during the entire period of the study. These damselfish also feed on benthic organisms, at which times they do not aggregate but rather are dispersed among the rocks. As in *C. atrilobata*, the midwater feeding aggregations rise above the rocks just before sunrise and descend to cover shortly after sunset. They are not in the open during the late stages of evening twilight, the early periods of morning twilight, or at night.

Ten specimens, 98 to 127 mm. long, collected late in the afternoon all had stomachs and intestines full of food. The bulk of the material was algae and crustaceans, although three had also ingested fish scales with attached bits of flesh. This last item is probably explained by the fact that *A. troschelii* frequently "cleans" other species. Such activity is not nearly so highly developed among members of this species as in *Heniochus nigrirostris*, however, and may be limited to removing necrotic tissue from the other animals. On one occasion I observed several individuals attempting to feed on a school of small (20 to 30 mm. long) herring, *Harengula thrissina*. An-

FIGURE 11.—A plankton-feeding aggregation of *Chromis atrilobata*.

FIGURE 12.—A plankton feeding aggregation of *Abudefduf troschelii*.

other time, I cut open holothurians at the surface and allowed the small commensal pearlfish *Encheliophis jordani* within to escape. As the pearlfish swam toward the bottom, they were invariably converged upon and consumed by several of these damselfish.

During dark nights these fish are inactive, but alert, while dispersed among the rocks. But when there is a bright moon they frequently move about near the bottom, often in small groups. Nevertheless, five individuals, 102 to 141 mm. long, speared between midnight and first morning light on nights when there was a full moon, provided no evidence of nocturnal feeding.

Conclusion

This damselfish is a diurnal omnivore, feeding on both midwater and benthic organisms. It engages in some "cleaning" of other species. Although active in aggregations when feeding on midwater organisms, it is dispersed among the rocks when feeding on benthic material.

Pomacentrus rectifraenum (Gill): Brown damselfish

Estimated period of direct observations: 10 hours.

Estimated period of general observations: 720 hours.

This small pomacentrid was extremely numerous during the entire study period on all the inshore rocky areas. Members of this strictly diurnal species are small; the adults seldom exceed 150 mm. in length. They seldom leave the immediate proximity of cover, and are generally variably dispersed among the rocks where they find their food. Ten specimens, 78 to 96 mm. long, collected for study of stomach contents indicate that they are largely herbivorous, feeding mostly on benthic algae. Yet soft coral and a small octopus in one showed that at least some animal material is ingested. After an active day among the rocks, they settle under cover on the bottom at dusk, where they remain inactive, but alert, until morning.

Conclusion

This diurnal omnivore feeds on benthic material—mostly algae but also some invertebrates. Activity is limited to rocky areas. These fish are variably dispersed among the rocks most of the time and do not move far from cover.

LITERATURE ON OTHER POMACENTRIDAE

Hiatt and Strasburg (1960) reported that *Chromis* and *Dascyllus* in the Marshall Islands form plankton-feeding aggregations above coral heads and dive among the sheltering coral branches when disturbed. Similarly, Eibl-Eibesfeldt (1962) noted that midwater aggregations of plankton-feeeding species of *Chromis* and *Dascyllus* in the Indian Ocean draw close together and dive into coral heads when threatened. Starck and Davis (1966) remarked that *Abudefduf saxatillis* and several species of *Chromis* in the Florida Keys are diurnal animals that are to a large extent particulate plankton feeders. In Hawaii, Gosline and Brock (1960) noted that most members of the genera *Dascyllus*, *Abudefduf*, and *Chromis* are "frequently seen forming a small cloud over coral of proper type. Generally these clouds disappear into the coral on approach." They reported that *Pomacentrus jenkinsi*, the only member of the genus in Hawaii, is "a solitary fish, living in holes in the reef and feeding on algae and perhaps detritus." They noted that food habits of Hawaiian pomacentrids "vary from herbivorous through omnivorous and carnivorous to detritus feeders." In the Marshall Islands, Hiatt and Strasburg (1960) found all six species of the genus *Pomacentrus* to be solitary bottom feeders. Five of these are primarily herbivores that take some animal material, but one is largely predaceous.

LABRIDAE

Bodianus diplotaenia (Gill): Pacific hogfish

Estimated period of direct observations: 12 hours.
Estimated period of general observations: 700 hours.

This is a relatively large wrasse; some individuals exceed 400 mm. in length. Perhaps associated with its larger size, adults of this species tend toward solitary habits or toward activity in groups of only a few individuals. They are active on all of the rocky areas near shore during the day and were present during the entire study.

Food is obtained from the rocky substrate. Five specimens, 250 to 400 mm. long, collected during the day, had fed on crustaceans, mollusks, and some small fishes. Earlier (Hobson, 1965a), I described how members of this species often closely follow the large scarid *Scarus perrico*, and other parrotfishes, to feed on scraps torn loose from the bottom by the browsing herbivore. They also capture prey driven from cover at these times.

Juveniles of *B. diplotaenia* aggregate in specific locations and are active cleaners. Other species seek out these locations to be cleaned.

At night they take shelter in the rocks, where they rest quietly until morning. Perhaps because they are relatively large, the adults are often content with semiexposed positions among the rocks. The small juveniles are rarely seen. The few individuals less than 50 mm. long observed were encased in mucous envelopes. In my report on diurnal-nocturnal activity (Hobson, 1965a), I remarked on nocturnal shelter-seeking habits in several Gulf of California labrids, and noted the formation of mucous envelopes by juveniles of *B. diplotaenia*. I discussed the possible value of these measures in deterring nocturnal predators.

Conclusion

This diurnal predator is active close to the rocks, where it feeds on a wide variety of benthic invertebrates and fishes. It tends toward solitary habits or activity in small groups. It often follows other species that disturb the substrate in order to capture small prey driven from cover. Juveniles are "cleaners." The species remains inactive among the rocks at night.

Thalassoma lucasanum (Gill): Rainbow wrasse (fig. 13)

Estimated period of direct observations: 20 hours.
Estimated period of general observations: 800 hours.

During the day this small, ubiquitous wrasse occurs on all the rocky areas along the shore. It was present during the entire program. When active more than a few centimeters from the substrate they aggregate, but are seldom far from cover and tend to be variably dispersed among the rocks much of the time.

In feeding, they usually pick small benthic organisms from the bottom. The diet of six specimens, 60 to 72 mm. long, collected at various times of the day included crustaceans, algae, and soft coral. Incidentally to their regular feeding activity these labrids engage in some cleaning of other species. This habit is particularly evident in juveniles, which often maintain stations around coral heads that are visited by other species.

All activity in members of this species is diurnal. During the night they lie quietly on their sides in crevices among the rocks, usually at least partly covered with sand.

Conclusion

The food of this diurnal predator includes crustaceans, algae, and soft coral. It engages in some cleaning, particularly as a juvenile. When away from cover it aggregates, but is usually variably dis-

FIGURE 13.—An aggregation of labrids, *Thalassoma lucasanum*, joined by a single *Runula azalea* (left center, with head turning away).

persed among the rocks. At night it rests quietly under cover.

Halichoeres dispilus (Günther): Chameleon wrasse

Estimated period of direct observations: 15 hours.

Estimated period of general observations: 700 hours.

During the day this wrasse, which is seldom over 100 mm. long, occurs in large numbers on all the inshore rocky areas. It was present throughout the duration of the study. When active away from cover, members of this species aggregate, but in their more customary location close to rocks they tend to be variably dispersed.

I did not examine their stomach contents, but their manner of picking at the substrate is essentially the same as that of *T. lucasanum*. When active among the rocks, the females and smaller males usually show a greenish body, with maroon head and caudal fin. The distinctively colored larger males are predominantly blue. They are often active out over open sand in areas adjacent to the rocks, a habitat seldom entered into by the other rock-dwelling labrids. Perhaps associated with its activity in these contrasting habitats, *H. dispilus* displays an ability to change color that I did not see in other labrids. When moving out over open sand from the rocks, it almost instantaneously assumes a light tan color, with a distinct dark longitudinal stripe running from just behind the head to its caudal fin. *H. dispilus* very often joins small aggregations of feeding goatfish *Mulloidichthys dentatus* that are foraging in the sand. As the goatfish dig about in the sand with their barbels, often burrowing their snouts up to their eyes, the accompanying wrasse intently regard the spot being disturbed,

and periodically dart forward to snatch up organisms uncovered. The labrids among these feeding goatfish often went unnoticed by me initially, largely because their color pattern was similar to that of the goatfish.

They are not active in the open at night. Although I did not see them in their resting spots, I assume they go under cover after dark.

Conclusion

This diurnal species feeds from the surface of rocks and sand. It aggregates when away from cover, but is usually variably dispersed among the rocks. It often joins aggregations of *Mulloidichthys* feeding over open sand near rocks to snatch up organisms uncovered by the goatfish. This species is capable of rapid change in color. It is not active in the open at night.

Halichoeres nicholsi (Jordan and Gilbert): Spinster wrasse

Estimated period of direct observations: 8 hours.

Estimated period of general observations: 620 hours.

This wrasse was present during the entire study period on all the rocky areas near shore. Although it may, like *B. diplotaenia*, exceed a length of 400 mm., very large individuals are infrequently observed; most individuals are less than 200 mm. long. Like other relatively large labrids, this species tends toward solitary habits or toward activity in groups of just a few individuals. It is not as numerous as the other labrids considered here, but, like the others, is active during the day.

I did not examine stomach contents, but this fish forages on the rocky substrate much as does *B. diplotaenia*. I often observed *H. nicholsi* following small foraging groups of *Mulloidichthys dentatus* over patches of sand among the rocks, snatching up small organisms driven from cover (fig. 14), in much the same manner as described above for the smaller *H. dispilus*. Unlike *H. dispilus*, *H. nicholsi* does not change color when moving back and forth between sand and rocky substrates, nor does it stray so far from rocky cover.

I did not observe members of this species at night; presumably they are inactive under cover, as are other labrids.

Conclusion

This diurnal species is active close to the rocks, where it feeds on benthic organisms. It tends toward solitary habits or activity in small groups. Often it follows other species that disturb the substrate to capture small prey driven from cover. It is inactive under sand or rocks at night.

Hemipteronotus pavoninus (Valenciennes): Pacific razorfish

Estimated period of direct observations: 7 hours.

Estimated period of general observations: 75 hours.

Although there is relatively little sign of life over the vast sandy expanses during the day, a few species are adapted to diurnal activity in this open habitat. This razorfish is one of these. Yet even this specialized labrid is most abundant where a rocky area lies nearby. It is solitary, but usually a number occur within a limited area, where they seldom move more than a few centimeters above the sand. My observations of this species are limited, as I only infrequently visited areas where it is abundant. Some individuals are relatively large, attaining a length of over 200 mm., but most are much smaller. I did not examine stomach contents, but have seen them dart forward from a hovering position to snatch some object in the sand. Despite the absence of rocks or other obvious shelter, these labrids are readily able to find refuge in the only cover available—the sand itself. Their ability to dive headfirst into the sand when threatened—dis-

FIGURE 14.—A labrid, *Halichoeres nicholsi*, closely follows a feeding goatfish, *Mulloidichthys dentatus*, to feed on organisms driven from cover as the goatfish disturbs the sand.

appearing in an instant—is remarkable. Furthermore, they are capable of lateral movement under the sand once buried. I did not see them in their regular diurnal locations after dark, when I believe they bury themselves in the sand.

Conclusion

This diurnal species feeds on or near the bottom. It inhabits the open sandy areas where it is largely solitary. It does not move away from the bottom, and takes shelter under the sand when threatened, and probably at night.

Hemipteronotus mundiceps (Gill): Cape razorfish

Estimated period of direct observations: 2 hours.

Estimated period of general observations: 28 hours.

Because I did not spend much time in the habitat of this razorfish during daylight, my observations concerning it are relatively limited. During the day, members of this species aggregate in midwater at some locations where water depth exceeds 6 to 10 m. over open sand. In the bay I observed them at Buena Vista and Punta Pescadero, where the largest were approximately 120 mm. long. I did not examine stomach contents, but their activity indicates that they are particulate plankton feeders. Like other small fishes that form midwater feeding aggregations, these labrids draw close together when threatened and dive toward the bottom. However, while most other fishes with this habit take shelter among rocks, these labrids deftly dive into the sand. They were not present in their regular diurnal locations when I worked there at night. Presumably they retire beneath the sand after dark.

Conclusion

This diurnal species feeds on plankton over open sandy bottom. It aggregates when in midwater, taking shelter under the sand when threatened, and probably also at night.

LITERATURE ON OTHER LABRIDAE

Labrids are widely recognized as strictly diurnal fishes. Breder (1948), Gosline and Brock (1960), Hobson (1965a), Longley (1916), Longley and Hildebrand (1941), Starck and Davis (1966), and others, have noted nocturnal shelter-seeking habits in various labrids.

BLENNIIDAE

Runula azalea Jordan and Bollman: Saber-tooth blenny

Estimated period of direct observations: 22 hours.
Estimated period of general observations: 700 hours.

Although this blenny is not particularly abundant in any one location, it occurred on all the inshore rocky areas during the entire study period. Members of this species are generally less than 75 mm. long. Much of the time they occupy abandoned mollusk tubes on the rocks, where they are highly territorial. At night they retire to these tubes, and during April 1964 I rarely saw them away from their tubes even in daylight, except when darting out to attack a passing fish. During all other periods of the study they were usually in the open during the day. This aggressive little fish attacks the posterior surface of larger fish that pass overhead (Hobson, 1965a). Usually these attacks are launched upward from a hovering position about 40 to 50 cm. above the rocks. As with other small fishes that are active away from shelter, they appear in aggregations when they are active above the bottom. However, the aggregations in which they usually appear are not of their own species, but rather those of the labrid *Thalassoma lucasanum*, which *R. azalea* superficially resembles (fig. 13). The resemblance of this blenny to the innocuous labrid with which it swims may enable it to go unnoticed as its victims approach. The blenny almost always attacks from below and behind its victims, and immediately on contact the larger fishes start and swim rapidly away. If the intended victim by chance turns toward the blenny during the latter's upward rush from the rocks, the attack is aborted. I have observed *Runula* making head-on approaches, but these were exceptional incidents.

I have seen a large school of *Haemulon sexfasciatum* numbering many hundred of individuals, ranging in length from about 250 to 350 mm., kept out over the sand, away from the rocks, by a group of only four to six of these tiny blennies, which were themselves only 75 mm. long. This was observed during August 1963, and the activity was recorded in my field notebook as follows:

> The blennies had stationed themselves over a rock at the edge of the sand while a large school of grunts hovered over the sand 20 yards away. Periodically the grunts began to edge slowly toward the rocks. When the grunts had approached to within a distance of 5 to 8 yards, the blennies left the rocks and, staying close to the bottom, swam out toward them. Although several of these blennies hesitated after moving out some distance, and turned back to the rocks before reaching the school, at least three to four made it all the way to a point directly under the grunts. From here they darted up and struck the posterior ventral surface of several grunts in the lower part of the school. The response of these individuals startled the entire school and sent them swimming rapidly out to their previous position 20 yards or so away from the rocks. With this, the blennies returned to the rocks, where they waited for the grunts to move in again. I remained at this location for over an hour, and during this time the sequence of activity described above was repeated four times.

George W. Barlow, of the University of California (personal communication), working in the Galapagos Islands, found that spawning in *Abudefduf troschelii* was sharply curtailed by the actions of *R. azalea* in areas where the latter were numerous. When attempting to spawn in such locations, the damselfish were almost invariably attacked by the blennies and driven back under cover, whenever the damselfish swam from the rocks into the open or descended from midwater to within about 1 m. of the bottom.

I examined the stomachs of four specimens, 35 to 52 mm. long, all of which were taken as they swam in aggregations above the rocks. I found only a mucoid substance in the stomachs of all four, suggesting that they derive nourishment from the mucous covering of the larger fishes.

Although these little predators possess a formidable set of canines, I doubt whether they are used in attacks on their large victims. I suspect they would find difficulty in extracting these saberlike teeth if embedded in their victims during such an attack. I have been bitten on the hand by these canines when handling these fish and found the wound painful. On the other hand, I have been struck on the legs by these fish hundreds of times when they responded to my swimming above them just as they do to larger fishes. Although the unexpected contact often startled me, I am quite certain that the canines were not employed. I believe that Eibl-Eibesfeldt (1955) was mistaken when he reported that *R. lineolata* (= *azalea*) uses its canines when it attacks large fish in the Galapagos Islands and "tears out chunks from their epidermis."

Conclusion

This diurnal predator is specialized to feed on mucous and perhaps elements of epidermis from larger fishes that it strikes primarily from below and behind. It remains inactive in mollusk tubes at night.

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LITERATURE ON OTHER BLENNIIDAE

Wickler (1960) reported that *Runula rhinorhynchus*, an Indo-Pacific species, feeds exclusively on mucous and skin particles from other species. Later (1961), Wickler noted that *R. rhinorhynchus* in aquariums attack larger fishes in the manner described above for *R. azalea*, and concluded that the victims of this species learn to avoid the blenny. He suggested that *R. rhinorhynchus* gains a position near its victims by hiding among the food of the larger fish, and attacks when the larger fish approaches to feed. My observations do not support such a theory for *R. azalea*. There was never any suggestion that larger fish attacked by *R. azalea* were approaching to feed on the labrids. They always appeared to be simply passing through the area. Wickler also observed *R. rhinorhynchus* stalking its prey along the bottom in aquariums, as *R. azalea* did in its interaction with *H. sexfasciatum* described above.

Strasburg (1960) felt that the large canines of *Runula goslinei* of Hawaii, and *R. tapeinosoma* of the western Pacific, are used in preying on smaller organisms. I saw no indication that *R. azalea* feeds on smaller organisms. Wickler (1960) noted that *R. rhinorhynchus* does not use its canines in feeding, but rather in territorial defense. Later (1961) Wickler reported that attacks by *R. rhinorhynchus* on other fishes in aquariums are often concentrated on areas around the eyes. He cited evidence that various color patterns of the prey influence the effectiveness of these attacks. I saw no evidence of attacks by *R. azalea* directed at the eyes of its victims, nor any indication that the attacks are influenced by color patterns.

CLINIDAE

Labrisomus xanti Gill: Rock blenny

Estimated period of direct observations: 4 hours.
Estimated period of general observations: 700 hours.

This small predator, attaining a maximum size of about 150 mm., was very numerous on all inshore rocky areas during the entire study. They rest motionless on the bottom during both day and night, usually under at least partial cover. Nevertheless, they seem to be in greater numbers in exposed positions during daylight than after dark. My sample of stomach contents was not large enough to recognize qualitative diurnal-nocturnal differences in food habits. Twenty specimens, 79 to 147 mm. long, were speared, most within 1 hour of sunrise or during midafternoon. Twelve of the nineteen individuals with food in their digestive tracts had fed on the arms of brittlestars (ophiuroids). Although brittlestars are generally under cover during the day and would be more accessible at night when they move out at least partly into the open, their arms are frequently exposed and portions might readily be taken by a small diurnally foraging fish. Crustaceans, mollusks, and soft coral composed the balance of the diet.

Labrisomus xanti illustrates the fact that whereas well-defined diurnal, nocturnal, or crepuscular feeding habits were readily recognizable in most of the fishes discussed here, such patterns were not so easily observed in many of the sedentary benthic species. The problem lies partly in the difficulty of recognizing periods of activity in species that are generally at least overtly inactive. This difficulty is especially acute at night, when a diving light is necessary to observe these small bottom dwellers against their dark surroundings. Earlier (Hobson, 1965a) I discussed the artificial effect induced by the diving light on the observed behavior in fishes.

Conclusion

This predator feeds largely on benthic invertebrates near the bottom, among the rocks. No conclusive evidence is available on the question of differential diurnal-nocturnal activity.

LITERATURE ON OTHER CLINIDAE

Starck and Davis (1966) reported that clinid blennies in the Florida Keys are inactive at night.

CHAENOPSIDAE

Acanthemblemaria macrospilus Brock: Barnacle blenny

Estimated period of direct observations: 16 hours.
Estimated period of general observations: 600 hours.

This chaenopsid occurred on all inshore rocky areas during the entire study. It is generally not over 50 mm. long. Members of this species inhabit abandoned mollusk tubes and barnacle tests on many of the rocks, with no more than one fish per tube or test. During the day the heads of these little fish protrude from their shelters. Periodically they dart out from their tubes to capture tiny free-swimming organisms that approach within distances of up to 0.5 m. The attack and immediate return to the tube are accomplished as one rapid and continuous movement. Occasionally they leave shelter and move around on the rock in the vicinity of their tubes; when returning, they always reenter their tube tail first. Although these fish are solitary and are isolated in their shelters, they occur in close proximity to many others of their species occupying similar shelters, usually on the same rock.

Food in four of seven specimens, 34 to 47 mm. long, taken with slurp gun within 1 hour after sunrise, was limted to crustacean fragments in the posterior part of the intestine; one other contained only a single mysid, apparently very recently ingested; the other two were empty. On the other

hand, all 14 specimens, 32 to 44 mm. long, collected between 1700 and sunset contained food in varying stages of digestion. Ingested items included minute crustaceans, gastropods, and coralline algae (the algae, found in two individuals, were probably taken incidentally with invertebrates). While no fish were found among this material, I observed one of these chaenopsids backing into its tube with the tail of a fish protruding from its mouth.

Occasionally I observed these fish at the entrance of their tubes at night, but usually I saw no sign of them after dark. Because of their small size and the fact that they quickly retract into their tubes when threatened, my failure to observe them at night could have reflected an avoidance of the light.

Conclusion

This diurnal predator inhabits abandoned mollusk tubes and barnacle tests on rock surfaces. Prey are mostly small free-swimming crustaceans that the chaenopsid captures by darting out from its tube. No good evidence of nocturnal activity was obtained.

Chaenopsis alepidota (Gilbert): Orangethroat pikeblenny (fig. 15)

Estimated period of direct observations: 8 hours.

Estimated period of general observations: 96 hours.

These pikeblennies appeared to be present during the entire study period, but relatively few observations were made. The largest I observed were about 100 mm. long. They inhabit abandoned worm tubes, often amid broken shell and fine gravel or cobble, on an open sandy bottom.

Although a number of individuals usually inhabit a limited area, members of this species are largely solitary. These fish vigorously defend a territory around

FIGURE 15.—A pike blenny, *Chaenopsis alepidota*, poised to strike at prey in the water above.

their tubes. They leave their tubes with greater frequency than do individuals of the rock-dwelling species *Acanthemblemaria macrospilus*, discussed above, and frequently occur among the cobble and broken shells on the bottom. I did not examine stomach contents, but pikeblennies are voracious predators that capture prey after darting from cover, or after stalking. I observed one individual back into its shelter with a fish in its mouth fully one-third its own size. On numerous occasions I saw them dart up among swarms of mysids, which often abound close to the bottom. *C. alepidota* stalks its prey in a distinctive manner. Propulsion is primarily from rapidly beating caudal and pectoral fins. The forward part of the body is usually held rigid, rod-straight, while the posterior part may undulate, or be flexed at an angle that sometimes approaches 90°. Prey are captured with a sudden thrust forward from this flexed position.

I saw no sign of these animals at night when making nocturnal visits to areas where they are active during the day.

Robins et al. (1959) presented some field observations by Conrad Limbaugh on *C. alepidota* in the Gulf of California.

Conclusion

This diurnal predator inhabits abandoned worm tubes in the sand, mostly over open sandy bottom covered with broken shell or small cobble. Prey are mostly free-swimming crustaceans captured by darting up from cover or after stalking. No evidence of nocturnal activity was obtained.

LITERATURE ON OTHER CHAENOPSIDAE

Robins et al. (1959) noted that the tropical Atlantic species *Chaenopsis ocellata* captured shrimps in aquariums with a sudden strike from a "semicoiled" attitude. Another pikeblenny, *C. limbaughi*, lives on a bottom of coral rubble in the Virgin Islands, where it preys primarily on small planktonic crustaceans (Robins and Randall, 1965). Starck and Davis (1966) found the chaenopsid fishes in the Florida Keys inactive at night.

GOBIIDAE

Gobiosoma digueti (Pellegrin): Redhead goby

Estimated period of direct observations: 2 hours.
Estimated period of general observations: 600 hours.

Although this small goby was far more abundant at some times than at others, it seemed to occur on the inshore rocky areas during the entire study. Members of this species are small, generally not over 35 mm. long, and rest in exposed positions on the rock surfaces—particularly surfaces that lie in the shadows. I did not examine their stomach contents, but they seem to be active cleaners. A large fish, such as *Lutjanus novemfasciatus* or *Gymnothorax castaneus*, resting in the shadows of a cave during the day will often have 20 or more of these tiny fish darting around on its body. These gobies also readily descend from the rocky walls of caves to land on a human who has entered. I did not see these fish at night, even by closely inspecting areas where they had been numerous during the day. Consequently, I believe they are largely diurnal, at least in regard to cleaning activity.

Conclusion

This diurnal species is active on the rocks, and engages in at least some cleaning of other species, particularly in caves. No evidence of nocturnal activity was observed.

LITERATURE ON OTHER GOBIIDAE

Starck and Davis (1966) reported that the gobies of the Florida Keys, including the cleaner *Elacatinus oceanops*, are inactive at night.

BALISTIDAE

Sufflamen verres (Gilbert and Starks): Brown triggerfish

Estimated period of direct observations: 36 hours.
Estimated period of general observations: 700 hours.

During the day this triggerfish is active on all the rocky areas, where it was present during the entire study. Members of this species tend toward solitary habits, but are frequently active in groups of a few individuals. They feed on a wide variety of benthic organisms inhabiting the rocky substrate. Six specimens, 230 to 255 mm. long, collected with spear, had fed on crustaceans, mollusks, soft corals, annelids, sea urchins, and algae. Once these triggerfish have worked over the part of a rock exposed above the sand, they may lie on their side and with rapid undulation of dorsal and anal fins produce water currents that carry away the sand next to the rock, exposing additional surface to feeding. In this manner rocks may be exposed to depths of over 30 cm. below the original sand line. They also feed on sand-burrowing animals after exposing them with a jet of water from the mouth (Hobson, 1965a).

At night these triggerfish lie quietly on their sides in crevices among the rocks, usually selecting a hole small enough so that the fish cannot be forcibly extracted when the long first spine of the dorsal fin is locked in an erect position (Hobson, 1965a).

Conclusion

This diurnal predator feeds on a wide variety of benthic organisms, many of which are buried in the sand and excavated through application of several specialized behavior patterns. It remains inactive under cover of rocks at night.

Crepuscular Species

ELOPIDAE

Elops affinis Regan: Machete (fig. 16)

Estimated period of direct observations: 12 hours.
Estimated period of general observations: 270 hours.

Machetes consistently occurred at Agua de la Costa and at Agua Caliente. My visits to both locations were largely limited to periods when herring were present along the beach, and I have no data on their occurrence during much of the year. Although they appeared frequently at other locations, I did not record these incidental sightings.

Whenever flatiron herring were present along the water's edge at Agua de la Costa, a large school of machetes, including several hundred individuals about 400 mm. long, moved slowly up and down the beach during the day, about 75 to 100 m. offshore from the herring. During the middle of the day, most or all of the machetes in the area were members of this large school.

Machetes usually prey on herring early in the morning and late in the evening. At these times the large school offshore has broken up into small groups of two to six individuals that actively seek prey near the beach. Evening predation becomes intense when herring have begun to move away from the water's edge into deeper water. The machetes are able to swim in under the herring at the greater depths, from where individual predators make explosive rushes into the herring above, often shooting through the school and emerging from the water. Thus intense feeding is limited to a period of approximately 20 minutes, beginning with the first abortive moves of the herring away from the beach, shortly after sunset, and ending about the

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FIGURE 16.—A school of machetes, *Elops affinis*.

time the bulk of the herring stream offshore.

In the morning, a lesser peak in predation occurs shortly before sunrise. I have only observed predawn activity from the beach, so my evaluation of relative intensity in predation is based on the incidence of individuals breaking the surface of the water. During the 2 hours after sunrise, many of them move offshore to form the large school in which they remain inactive during the day. Many others stay inshore during this period, patrolling along the outer edge of the herring school in their small foraging groups. Periodically members of these groups swing in among the herring with a sudden burst of speed, then veer upward, describing a "loop" that often breaks the surface of the water at its apex before returning the machete to its original patrolling course along the outer edge of the school. Thus we again see the attack from below that characterizes the evening feeding maneuvers. Three hours after sunrise little of this activity occurs. Most of the matchetes have by then joined the large school offshore. I did not observe this predator at night.

Conclusion

The machete is a crepuscular predator, at least when herring are available, and is active in groups of two to six individuals. It forms large schools during a midday period of inactivity.

SERRANIDAE

Mycteroperca rosacea (Streets) Leopard cabrilla (fig. 17)

Estimated period of direct observations: 182 hours.

Estimated period of general observations: 850 hours.

I selected the cabrilla for intensive study because its habits are readily observed, and because it is probably the most ubiquitous

FIGURE 17.—Cabrilla, *Mycteroperca rosacea*. One individual represents the golden form of this species.

medium-sized predator in the area. Members of this species were present on all the inshore rocky areas during the entire program. They attain a length of about 700 mm.

Stability of populations.—Populations of this grouper inhabiting each of the isolated rocky areas seem to remain relatively constant, but my data on this point are weak. A limited tagging effort, in which 56 individuals were marked with distinctively colored dart tags at three locations, showed no evidence of movement from one area of rocks to another. However, only three, or perhaps four, marked fish were seen after the second week following tagging, although these were observed repeatedly over the next several years. I found a number of tags lying on the bottom, showing that at least some had been lost. Fish seen carrying tags were within 50 m. of the spot where they had been marked, including two individuals sighted 3 years after tagging.

Extensive tagging programs carried out in other areas (Randall, 1961; Springer and McErlean, 1962; Young, 1963) have indicated that the movements of at least most serranids inhabiting inshore reefs are generally limited.

Limited observations at depths exceeding 50 m. suggest that *M. rosacea* does not frequent deeper water. Although cabrilla are abundant in shallow water at both Punta Pescadero and Los Frailes (the latter location being about 40 km. south of the study area), I did not see them during several dives below 50 m. at these locations. Similarly, R. H. Rosenblatt, of Scripps Institution of Oceanography (personal communication), noted the absence of cabrilla below about 50 m. when

diving in the Cousteau diving saucer at Cabo San Lucas, an area where these Serranids are numerous in shallow water.

Size and behavior.—Behavior changes rather abruptly when cabrillas are 250 to 300 mm. long. I consider the two size groups separately, referring to cabrilla exceeding a length of approximately 250 to 300 mm. as large and those under this size as small.

Predation by large cabrilla

PREDATION ON FLATIRON HERRING

Predilection for herring.—When present, *Hærengula thrissina* constitutes essentially the entire food source of the large cabrilla. Fifty-three cabrilla over 250 mm. long were speared offshore from herring schools at three different locations (Agua de la Costa, Buena Vista, and Punta Soledad) during October and November 1962. All but two of the 142 identifiable prey specimens taken from these cabrilla were either flatiron herring or juvenile anchovettas *Cetengraulis mysticetus*, a species that occasionally schools with the herring. The two exceptions included one 175-mm. specimen of *Selar crumenophthalmus*, taken from a 605-mm. cabrilla, and one 75-mm. specimen of *Ophioblennius steindachneri*, from a 390-mm. cabrilla. During this same period, 10 cabrilla over 250 mm. were speared while actually under the herring schools at these locations. All 30 identifiable prey specimens found in the stomachs of the five containing food were either herring or anchovettas. Furthermore, none of the unidentifiable fragments found among stomach contents suggested ingestion of prey other than herring or anchovettas.

This serranid is called cabrilla sardinera in some regions of the Gulf of California in reference to its predilection for sardinas, as herring are called there.

Pattern of predation on flatiron herring.—When a large herring school is present in the area, along with the occasional accompanying anchovettas, the habits in members of the cabrilla population become strikingly uniform as they all turn to this source of prey.

Little predation occurs during midday, when the large cabrilla on a given rock area gather in one to several relatively inactive concentrations that usually form at a particular point along the offshore edge of the rocks. These concentrations occur in the same locations each day as long as herring school inshore. When approaching these cabrilla, I often found them in a rather tight midwater group. However, I was never able to closely observe these associations, because as I neared, still at the outer limit of visibility, they always became alerted and fanned out to the rocks below. As long as I remained in the area they stayed among the rocks, swimming actively about but nevertheless remaining together.

About 2 to 3 hours before sunset the cabrilla in these concentrations begin moving inshore toward the herring. They do not all move in together, but rather a few at a time, with the numbers increasing sharply at the approach of sunset.

After moving in under the herring, staying close to the bottom, they usually select resting spots offering at least partial concealment, for example at the base of an overhanging rock. Here they rest motionless, their bodies often inclined somewhat so as to be more or less oriented toward the herring above. From these positions the cabrilla periodically make explosive rushes up among the herring, turn abruptly, and return to their resting spots on the bottom.

Although cabrilla may operate individually, they tend to form loose feeding aggregations. This is particularly true during morning and evening twilight, when

both in number and in size the cabrilla operating under herring schools attain maximum proportions, and feeding intensity also reaches a peak. At these times in particular, cabrilla leap out of the water while feeding. This is a spectacular action, for over 20 cabrilla may be in the air simultaneously. The incidence of these mass jumps reflects the increase in feeding intensity, and was recorded from the beach at Buena Vista (fig. 18).

Feeding continues to increase in intensity for a period after sunset. This is indicated not only by incidence of jumping as viewed from the surface, but also by underwater observations. Activity of birds that prey on the herring also increases during this period, and often mass feeding rushes by cabrilla occur where a pelican has just dived into the water.

Feeding reaches a peak at about the time the herring move offshore toward their nocturnal feeding grounds, about 20 minutes after sunset. In the observations at Buena Vista during September 1962 no jumping from the water by cabrilla oc-

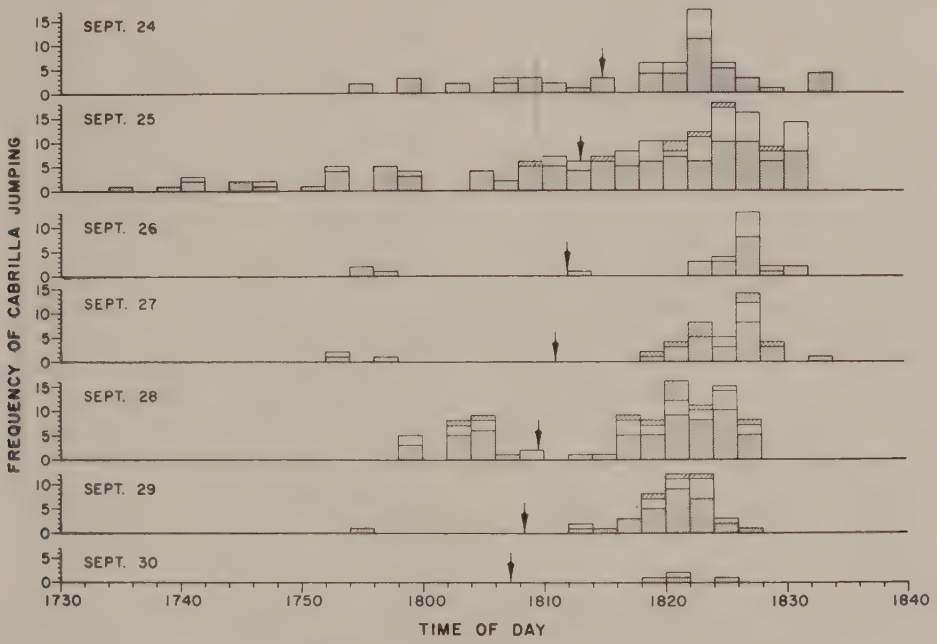

FIGURE 18.—Incidence of cabrilla jumping from the water amid a flatiron herring school in the evening at Buena Vista.

Method of making observations: Incidence of cabrilla jumping from the water was observed from the beach. Observations were made over 2-hour periods, 1700 to 1900, on 7 consecutive days, 24–30 September, 1962. A mark was recorded, with time of day, whenever a cabrilla left the water. If two to six cabrilla jumped simultaneously, a distinctive mark indicated this fact. If seven or more cabrilla were in the air at one time this too was recorded with a distinctive mark. These observations, grouped into 2-minute intervals and presented graphically offer this picture of jumping incidence in time.

Symbols in figure: Stippled area of bars=frequency of jumps involving a single cabrilla; white area of bars=frequency of jumps involving two to seven cabrilla; hatched area of bars=frequency of jumps involving more than seven cabrilla; inverted arrows indicate time of sunset.

curred after the herring school had left the beach. The incidence of jumping during the herring's offshore migration on different occasions was highly variable. Some of the factors influencing this variability are discussed below.

Cabrilla follow the herring for a short distance offshore, but I saw no evidence that they maintain contact with the prey school much beyond the outer edge of the rocks.

During the night cabrilla are relatively inactive, moving about over the rocks when there is a bright moon, but resting on the bottom among the rocks on dark nights. I have no good evidence of nocturnal feeding by individuals inhabiting areas where herring were available during the day.

In the morning, many cabrilla follow the herring returning over the rocks to their daytime position near the beach, and feeding cabrilla jump during this period (fig. 19). However, jumping in the morning generally does not reach the high level of intensity often achieved in the evening.

At dawn most cabrilla on the rock area are under the herring school, and predation is intense. Yet even at times of peak feeding inshore there are always at least a few cabrilla offshore—usually near the locations assumed later by the midday concentrations. Counts made of cabrilla in different areas at Agua de la Costa during October 1962 showed that about 3 percent of the cabrilla at the offshore concentration site during midday were there at sunrise.

Shortly after sunrise, cabrilla feeding activity begins to decline, and individuals begin moving offshore. This offshore movement continues throughout the morning; most of the cabrilla join the offshore concentration 2 to 3 hours after sunrise. By midday most have joined the relatively inactive associations at the outer edge of the rocks.

At Agua de la Costa during October and November 1962 the number of cabrilla under a segment of the herring school at different times of day, compared with the number at the offshore edge of the rocks at the same times, clearly showed the inshore-offshore movements of these predators (fig. 20).

Midday activity of cabrilla.—Although there are always at least a few cabrilla under the herring school through midday, they feed infrequently. The following observation, quoted from my field notes, records some midday activity in 2 m. of water near the beach at Punta Soledad.

I floated motionless at the surface among the herring school for 2 hours, continuously observ-

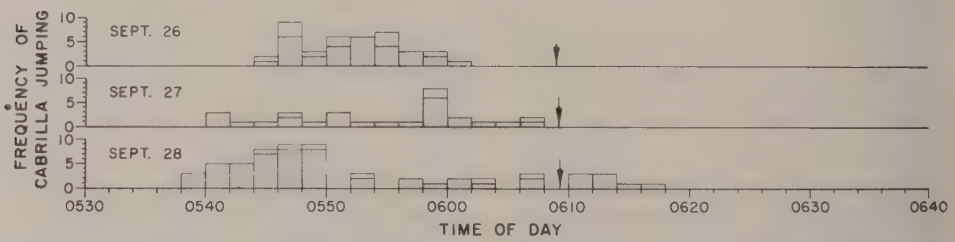

FIGURE 19.—Incidence of cabrilla jumping from the water amid a flatiron herring school in the morning at Buena Vista.

Method of making observations: As reported for fig. 18, except that observations were made over 2-hour periods, between 0500 and 0700, each morning on 3 consecutive days, 26–28 September, 1962.

Symbols in figure: As in fig. 18, except that inverted arrows indicate time of sunrise.

ing a single cabrilla, about 300 mm. long. It was stationed on the bottom nearby, intently regarding the herring above. During this period the cabrilla made just three rushes at the herring, with each rush coming as a wave of disturbance passed through the school following the entry of a diving pelican into the water. This disturbance resulted in a number of herring dropping below the school, seemingly disoriented, and each time the cabrilla directed its attack at these displaced herring. After 2 hours I moved for the first time, and dived to the bottom. The herring around me became alarmed at my sudden movement, and several followed me down, swimming in a small disorganized group approximately 1 to 2 feet in front of my face plate. The cabrilla immediately responded by making two rushes at the little group in rapid succession, each time coming within 2 feet of my face.

Predation and the evening offshore flatiron herring migration.—At Buena Vista and some other areas, as described above, predation reached a peak in intensity just before the offshore herring migration in

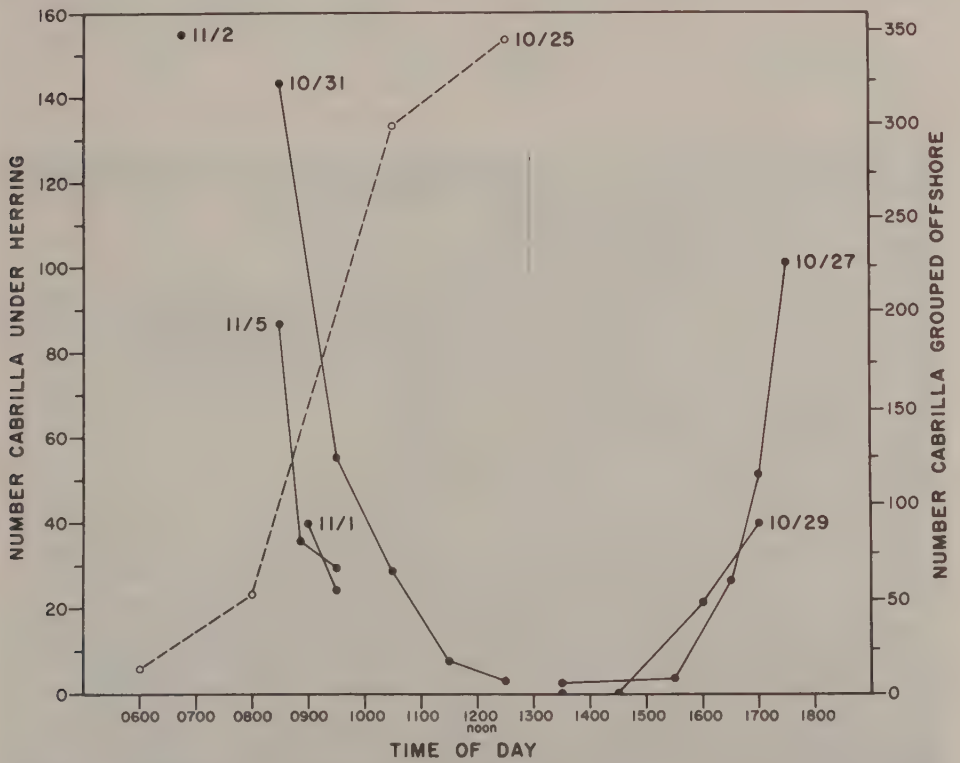

FIGURE 20.—Incidence of cabrilla under a flatiron herring school at Agua de la Costa at different times of day, compared with incidence of cabrilla in offshore concentrations at the same time.

Method of making observations: Underwater counts were made of cabrilla along the outer edge of the herring school at different times of day between 22 October and 11 November, 1962. All counts were made over the same course of about 100 m. between two points on the beach when water was calm and visibility good. These observations are presented in the figure as black circles, with a solid line connecting observations made on any one day. The date is indicated next to the first or last observation made that day.

Incidence of cabrilla grouped offshore at different times of day on 25 October, 1962, as observed swimming along the outer edge of the rocks, is also presented. These data are presented in the figure as open circles connected by a broken line.

the evening. On other occasions intensive predation occurred during the move away from the beach.

Some factors influencing relative vulnerability of herring during this migration became evident at Punta Soledad during October 1962. The distribution of sand over the bottom off the point was such that the pattern of exposed rocks (fig. 21) offshore strongly influenced the activity of both herring and predators.

Over a period of 10 days, herring were present diurnally over rocks at the water's edge. I observed activity at this point on six different evenings, and on every occasion the sequence of events was essentially the same. Although predation on herring was heavy during twilight, I observed relatively few cabrilla jump out of the water in their characteristic manner, despite the large numbers present. Observations were made from different vantage points on the different evenings, and on two occasions I was so situated as to be unable to note precisely when the herring began moving away from the beach. On the other four occasions I observed the initial offshore movement and found the times involved to be as follows: 1813 on October 12, 1810 on October 14, 1810 on October 15, and 1809 on October 19.

FIGURE 21.—The area offshore at Punta Soledad during October–November, 1962, showing route followed by flatiron herring during the evening migration. Herring schooled along the beach each day (point A) and migrated offshore each evening over the narrow rocky pathway (arrow). Confusion in ranks of the school, as described in the text, resulted upon encountering the rock-sand interface (point B).

The offshore movement took place about 20 minutes after sunset, as it did during the previous month 5 km. to the north at Buena Vista.

From a position on a hill overlooking the beach, I was able to observe early indications of restlessness in the herring not evident from water level. At these times small subschools within the main body of herring began seemingly random movements independent of the main body of the school. These movements had no recognizable direction, as the fish sometimes headed closer to the beach and at other times briefly headed offshore from the main body.

After a short period of this seemingly directionless activity, the whole school began to move together. Rather than swim out over the open sandy bottom that lay immediately offshore from their diurnal schooling location, the herring funneled out over a narrow rocky pathway that led at a 45° angle from the shoreline (fig. 21). This pathway lay in a straight course for about 75 m. then abruptly turned 45° to lead directly offshore. Water depth at the turn was about 5 m. As the first herring arrived at this sharp turn, they continued briefly in a straight line out over the sand. However, they quickly reversed direction and swam back toward the rocks. This maneuver led them back into the face of the vast numbers of herring coming out behind them. The result was a localized breakdown in the structure of the school and a point of mass confusion. Large predators were accompanying the herring offshore, and every evening the surface of the water at this point became a froth of activity as the predators immediately converged on the disorganized segment of the school. Predators active here, in addition to cabrilla, included *Elops affinis*, *Caranx hippos caninus*, *Nematistius pectoralis*, and the sierra mackerel, *Scomberomorus sierra*. The most intensive predation I observed during the entire study was witnessed on these six occasions.

In addition to watching this sequence of events from the hill, I observed it once from the beach, twice I accompanied the herring along the rocky pathway from their diurnal location near the beach, and twice I sat on the bottom at the point of the abrupt turn in the pathway and waited for the herring to arrive.

As the herring funneled out along the narrow rocky pathway, small segments of the school were diverted down outcroppings in the rocky pathway which proved to be "dead ends." The situation which the entire school was to face farther offshore was met by these small groups and with a similar result, as predators accompanying the school converged on points of confusion at these dead ends. However, predation at these points was on a realtively small scale and was generally not evident from the surface.

The point of mass confusion and intense predation existed for a period of several minutes. After this time the herring apparently adjusted to the 45° turn in their course. The point of confusion immediately disappeared as the school made the turn smoothly, and predation abruptly subsided. I observed no further incident as the herring continued offshore from this point.

Food studies.—Several aspects of predatory behavior in cabrilla are better understood after examining digestive tract contents.

I made estimates of the relative degree of digestive action on herring, along with a few anchovettas, in the stomachs of the 53 cabrilla, 254 to 645 mm. long, speared offshore from herring schools at different times of day (fig. 22). No recently ingested prey were found in cabrilla taken during

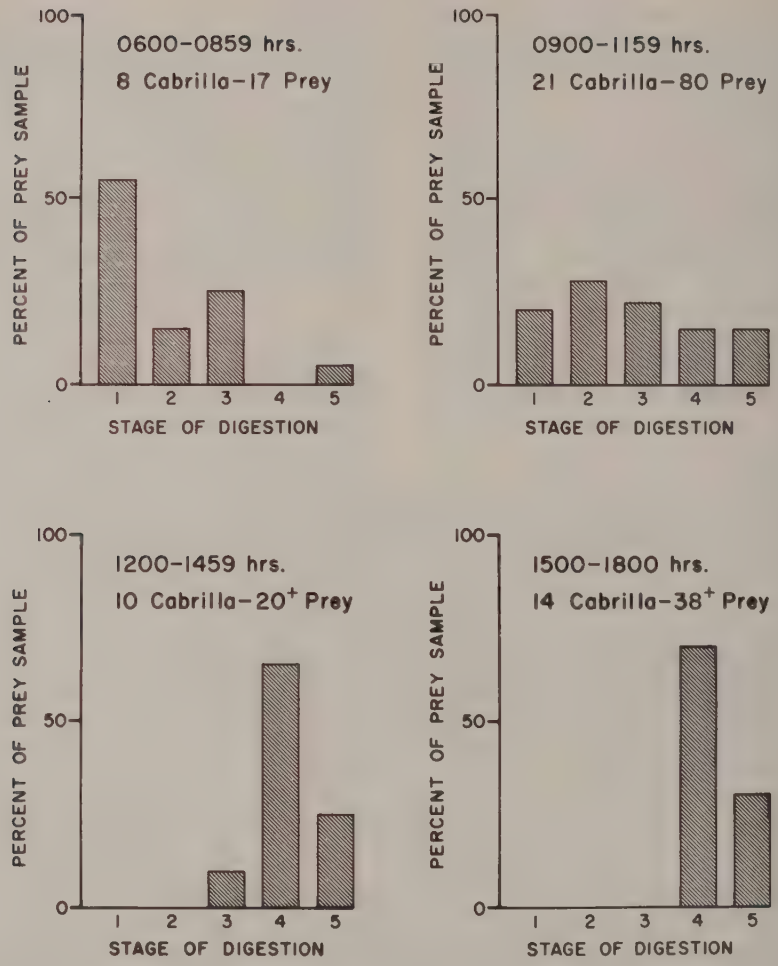

FIGURE 22.—Relative degree of digestion undergone by flatiron herring in stomachs of cabrilla taken offshore from herring schools at Agua de la Costa, Buena Vista, and Punta Soledad, during October and November, 1962.

Method of making observations: Prey were examined after being removed from stomachs of cabrilla speared at different times of day. Each prey specimen was assigned to one of five arbitrarily defined classes based on a rough estimate of the relative degree of digestion it had undergone. The five classes, with defining criteria:

1. Fresh.—Little or no digestion. Apparently very recently ingested.
2. Slight digestion.—Major morphological features intact, but signs of digestive action clearly in evidence.
3. Moderate digestion.—Identification and measurements still readily made, but damage due to digestion extensive.
4. Considerable digestion.—Only gross identification possible. Measurements only estimates.
5. Advanced digestion.—Fragments only.

All were taken offshore before sunset, so probably none of those moving inshore to feed late in the afternoon were sampled.

the afternoon. Rather, as the day progressed, there was a sharp increase in the relative number of well-digested prey in the samples. Furthermore, only six (21 percent) of 29 cabrilla taken during the morning had empty stomachs, as compared with 12 (50 percent) of 24 having empty stomachs during the afternoon.

The number of prey in cabrilla offshore from herring schools during the day was highly variable. Some contained as many as 19 herring in their stomachs; others had apparently moved offshore after capturing just one. In specimens where the number of prey in the stomachs could be ascertained, the arithmetic mean was 4.5, while the mode was just 1. Apparently some cabrilla move offshore despite no success in capturing prey, judging from the number of cabrilla offshore in the morning with empty stomachs. Although it was not possible to be sure cabrilla with empty stomachs had as yet been inshore under the herring school that morning, one cabrilla with an empty stomach was taken during midmorning heading offshore midway between the herring school and the offshore cabrilla concentration.

I found no correlation between size or number of prey and the size of the cabrilla in whose stomachs they were found. Large cabrilla containing herring were between 255 and 645 mm. long. Throughout this size range, size frequency of prey was essentially that of the herring school itself. Furthermore, the cabrilla containing 19 prey was itself only 495 mm. long, whereas the largest cabrilla taken with herring in its stomach (645 mm.) contained only four specimens. In both of these cabrilla the herring were between 60 and 80 mm. long.

PREDATION WHEN FLATIRON HERRING ARE ABSENT

Predilection for schooling fishes.—When herring are not available, cabrilla turn to a wide variety of other prey, primarily to other species which, like the herring, form dense, relatively inactive schools near shore during daylight. Ninety-nine cabrilla over 250 mm. long were speared for stomach content analysis when no herring were available. The 62 specimens with food in their stomachs had fed entirely on fishes. Of 48 identifiable prey specimens found among the stomach contents of these cabrilla, 37, or 82.5 percent, were from eight species which, though representing four different families (Mullidae, Carangidae, Pomadasyidae, and Sciaenidae), strikingly resemble herring in many of their general habits. These species are *Mulloidichthys dentatus*, *Selar crumenophthalmus*, *Xenichthys xanti*, *Haemulon sexfasciatum*, *Lythrulon flaviguttatum*, *Microlepidotus inornatus*, *Orthostoechus maculicauda*, and *Umbrina xanti*. In addition to schooling near shore during the day, members of these species, like herring, disperse to feed at nightfall, often after moving a considerable distance offshore.

As when preying on herring, cabrilla concentrate their feeding on these fishes during early morning and late afternoon and evening. The periods of maximum feeding intensity occur during twilight—just before dispersal of the large schools in the evening and just after they have reformed in the morning. But the pattern is not so clearly defined as when herring are the prey. Predation on these fishes does not involve simultaneous movements by large segments of the cabrilla population, as it does when cabrilla feed on the herring. Now predation is directed against a number of different prey, which the cabrilla find in a variety of localities around them.

The number of cabrilla increases during early morning and late afternoon beneath the schools of *Selar crumenophthalmus*, *Microlepidotus inornatus*, and *Lythrulon flaviguttatum* located in 3 to 4 m. of water

over relatively open bottom at Buena Vista. These cabrilla move out from among the adjacent rocks in a manner suggesting their inshore movement when making contact with herring. This movement is not nearly so striking as the inshore-offshore movement characteristic of predation on herring, and at any hour of the day a considerable number of cabrilla may be under the schools. I seldom observed cabrilla in the immediate vicinity of the small schools of *X. xanti* near the beach, but these prey too were taken from cabrilla stomachs.

As schools of *Haemulon sexfasciatum* and *Mulloidichthys dentatus* generally occur at the outer edge of the rocks in areas frequented by large cabrilla during the cabrilla's inactive periods, it is not surprising that the predators are proximate to these schools throughout the day. Nevertheless, as with predation on other schooling species, most feeding occurs during early morning and late afternoon. Midday feeding is limited to occasional rushes up into the school by one or several cabrilla. In general, I did not observe much predation on schools of *H. sexfasciatum* by cabrilla, perhaps because of the relatively large size of this prey.

Predation on juvenile pomadasyids.—During late fall and early winter, cabrilla turn to the juvenile pomadasyids that appear in exceptionally large numbers at water's edge. At this time activity of the predators suggests their feeding habits when herring are present. Although juvenile pomadasyids do not monopolize food habits of cabrilla, as do the herring, they do induce inshore-offshore movements of cabrilla during late afternoon and early morning. However, as the juvenile pomadasyids form many relatively small, discrete schools at different points along the shore, the efforts of the cabrilla are correspondingly dispersed and, as a rule, large feeding aggregations do not form. Furthermore, they do not jump from the water while feeding on these prey as frequently as when preying on herring.

Other prey.—With few exceptions, all large cabrilla sampled were taken from areas where at least some of the schooling fishes just mentioned were present. Although these species dominate the cabrilla's diet, prey also are taken from among the many other smaller species. The numerous labrids, pomacentrids, and others were represented in the sampling by 11 prey specimens, representing less than 22.5 percent of the identifiable material taken from cabrilla stomachs.

Two cabrilla had each fed on single specimens of *Abudefduf troschelii*. As this plankton-feeding omnivore rises into midwater, or to a point just under the surface, as early as 20 minutes before sunrise, it might well be exploited by cabrilla during the later periods of morning twilight by means of an attack from below. This may have occurred in the capture of one of the two specimens of *A. troschelii*, an individual 126 mm. long that was moderately digested when taken from the stomach of a cabrilla at 0815. The other, a specimen 108 mm. long, showed no evidence of digestive action when taken from a cabrilla at 0915, indicating it had very recently been ingested.

A third cabrilla had fed on a surgeonfish, *Prionurus punctatus*, 89 mm. long. This prey specimen was extensively digested when recovered at 1330. *P. punctatus* of this size generally swim in small groups of four to six individuals close to rocky bottom.

A single specimen of *Pomacentrus rectifraenum*, 98 mm. long, was moderately digested when recovered at 1300, suggesting it had been captured while among the rocks some time earlier that morning.

The stomach contents of six other cabrilla may suggest a more radical departure from the more usual feeding behavior. Each contained a single squirrel-

fish, *Myripristis leiognathus*. These six prey specimens, 45 to 127 mm. long, all taken from cabrilla between 1000 and 1200, were only moderately digested. They were probably captured under rocky cover where squirrelfish retreat during the day, rather than in the open where they actively feed at night.

In the only observed incidence of cannibalism, one of the cabrilla containing a squirrelfish had also ingested a small member of its own species. This prey was moderately digested when taken from the cabrilla at 1045.

On one occasion a cabrilla about 350 mm. long rushed from the bottom into a small aggregation of labrids, *Halichoeres* sp., which were active above a large rock. When the cabrilla returned to its resting spot on the bottom, it remained motionless for a moment, with the head of one of the labrids, an individual about 125 mm. long, protruding from its mouth. Then, following an abrupt movement of its head, the tail of the prey protruded. At this point the cabrilla darted out of sight beneath a nearby rock. This incident occurred during midmorning in 3 m. of water over rocky bottom at Punta Anhelo. The ability of the cabrilla to shift the position of prey in its mouth, presumably in order to swallow it head first, is probably a well-developed manipulation. The difficulties resulting in an attempt to swallow a relatively large spiny-rayed fish tail first are obvious.

Although the pattern of predation on nonschooling fishes remains unclear, I did not observe evidence of crepuscular peaks in feeding activity, as was evident in predation on the schooling species. However, cabrilla continued more active during early morning and late afternoon than during midday.

The presence of well-digested fish remains in a number of cabrilla during early morning strongly suggests at least some nocturnal feeding.

Conclusion (large cabrilla)

These serranids are chiefly crepuscular predators when feeding on schooling fishes, their major prey. Twilight feeding is not marked when they feed on nonschooling prey. They are seldom active during midday in either case. These large members of the species are strictly piscivorous. At least some nocturnal feeding occurs.

Predation by small cabrilla

Although the larger cabrilla are generally concentrated at the outer edge of the rocks during midday, the smaller individuals are usually scattered over the bottom throughout the rocky area, often in groups of 2 to 10 individuals, where they usually remain close to the substrate.

Sixty-nine cabrilla under 250 mm. were speared for stomach analysis. The stomachs of 31 of these specimens were empty. Of the 35 identifiable items taken from the stomachs of the other 38 individuals, 12 were herring, one was an 88 mm. wrasse, *Halichoeres dispilus*, and the other 22 were benthic fishes and crustaceans between 10 and 50 mm. long. Benthic fishes taken included blennies, clinids, gobies, tripterygiids, and dactyloscopids. These prey were usually not readily identified to species, as damage resulting from digestive action quickly rendered specific characters in these very small fishes (average length approximately 20 mm.) indistinguishable. It seems generally true that crustaceans comprise a larger part of the diet in small and young serranids than in larger individuals (Smith, 1961). This is probably related to the relative abundance of crustaceans within the proper size range. Randall and Brock (1960) noted that whereas the small Indo-Pacific serranid *Epinephelus merra* preys largely on crustaceans through most of the year, it switches to juvenile fish when these become abundant during the summer.

Smaller cabrilla often closely accompany

a large *Bodianus diplotaenia* when the latter uproots the cover on rocky substrate in search of prey. During this activity the accompanying cabrilla hovers within a few centimeters of the labrid's jaws, intently regarding the spot being disturbed, and quickly comsumes small fish or crustaceans driven from cover.

The large cabrilla apparently do not regard these very small bethic fishes and crustaceans as prey. Considering the manner in which cabrilla stalk and attack individuals, and the energy thus expended in their capture, such small prey may be an unsuitable food source because of their relatively low nutritional return.

These small benthic fishes do not change their overt behavior in the presence of large cabrilla and apparently do not regard them as a threat. This observation is supported by the fact that large cabrilla are actually used as shields behind which cornetfish *Fistularia petimba* approach the same fishes preyed upon by small cabrilla. Upon gaining a position close to such prey in this manner, the cornetfish darts out from behind the cabrilla to make the capture. If such a technique is effective, and its very existence suggests that it is, then it follows that prey so stalked by the cornetfish do not regard the large cabrilla as a predator.

Although the small cabrilla feed primarily during the day, some nocturnal feeding occurs on dark nights as well as nights when there is a bright moon. Of 20 specimens shorter than 300 mm. speared between 1 hour before and 30 minutes after sunrise, seven (35 percent) contained at least moderately digested fishes, most, if not all, of which had probably been ingested during the previous night. Of 51 speared between midmorning and sunset, 34 (67 percent) contained food. Twenty-eight (82 percent) had fed exclusively on fish, 1 (3 percent) had fed exclusively on crustaceans, and 5 (15 percent) had ingested both fish and crustaceans. The crepuscular peaks in feeding intensity noted in larger cabrilla were not evident in the smaller individuals, with the possible exception of when they preyed on herring.

Conclusion (small cabrilla)

These predators feed variably on crustaceans as well as smaller fishes. Most prey are benthic organisms among the rocks, although flatiron herring and other suitably small schooling fishes are taken when available. Crepuscular habits are especially marked only when preying on schooling fishes. Little feeding occurs during midday. Some prey are taken at night.

NEMATISTIIDAE

Nematistius pectoralis Gill: Roosterfish

Estimated period of direct observations: 13 hours.
Estimated period of general observations: 600 hours.

Roosterfish are present in variable numbers during most of the year, although they may be largely absent during winter and early spring. These big predators, often exceeding a length of 700 mm., do not seem to be restricted to any one point along the shoreline as they range along the beaches. Nevertheless, many with recognizable markings are seen in the same vicinity for at least several weeks at a time, and they are consistently more abundant in some areas than in others.

The appearance of roosterfish often cause members of such species as *Haemulon sexfasciatum* to rush abruptly together to form a very tight school. The large diurnal schools of this grunt frequently become variably dispersed during the day, as when they visit a cleaning station. On one occasion, a group of the pomadasyids that were dispersed among a group of active cleaners abruptly terminated the cleaning and drew into a tight school when a large roosterfish appeared (Hobson, 1965a).

Similar observations were made at other times, and on these occasions the intruder usually was a roosterfish. However, sometimes roosterfish pass quietly through an area without eliciting a noticeable response in pomadasyids.

This study indicated that the prey most frequently exploited by roosterfish in the study area are members of *Selar*, *Microlepidotus*, and *Lythrulon* schools. On many days, roosterfish are in the immediate vicinity of these schools from the time the schools arrive inshore in the morning, until just before they move offshore in the evening. The predators slowly patrol the area, circling and occasionally passing through the schools. Members of the schools separate before the advancing predator as it enters among them, then close in behind the big fish after it has passed. As long as the movements of the predator remain unhurried, the prey show no overt sign of concern beyond maintaining a distance of a meter or so between themselves and the larger fish (fig. 23). Abrupt moves by the predator immediately elicit an evasive response in the prey. The distance between predator and prey abruptly increases as the prey radiate out before the charging predator, and a void thus materializes around the bigger fish (fig. 24). As soon as the predator has passed, the prey close ranks. During midday, aggressive maneuvers by roosterfish are infrequent. At this time groups of the large fish often circle about a school of grunts or bigeye scads for several hours without making an aggressive move. Occasionally one or all may suddenly rush into the school. Despite minimal feeding activity during midday, the predators readily feed during this period if presented with an opportunity. This was demonstrated repeatedly by injuring one of

FIGURE 23.—A school of scad showing little overt concern as long as the roosterfish swimming among them makes no abrupt movement.

FIGURE 24.—A void forms around an attacking roosterfish as schooling flatiron herring radiate out before the charging predator.

the schooling fishes in such a way that it swam erratically and was unable to maintain its normal station in the school. Such individuals were quickly sensed by the alert predators circling the school and taken.

Incidence of predation increases early and late in the day. In its predatory maneuvers, this piscivore usually veers into the school from its patrolling course around the periphery, and attempts to run down the prey with a burst of speed. The black bars on the body of the roosterfish, clearly seen at all times, become especially evident when the fish attacks. In addition, its highly developed, comblike dorsal fin is frequently erected as the big fish rushes into a prey school. During periods of intensive predation, the schools of *Selar* and pomadasyids sometimes move right in to the water's edge, occasionally stranding during their evasive maneuvers.

Far less frequently than they attack grunts and scad, roosterfish turn to the flatiron herring schools next to the beach. They often experience difficulty maneuvering, however, and on three occasions I saw roosterfish struggling in the rocky shallows at the water's edge, attempting to regain deeper water after their explosive rushes through a herring school had stranded them.

Conclusion

The roosterfish is a crepuscular predator, at least when preying on the schools of fishes near shore. Most activity is centered around schools of grunts and scads in depths of 3 to 4 m.

CARANGIDAE

Caranx hippos caninus Günther: Toro (fig. 25)

Estimated period of direct observations: 23 hours.
Estimated period of general observations: 600 hours.

Toros, many over 500 mm. long, were present through most of the year, although they seemed to be absent during late winter and early spring. I did not see them upon my arrival in early April 1964, but near the end of the month I made a few scattered sightings. After a few days I observed a single school that must have contained well over 1,000 individuals, all longer than about 400 mm. Subsequently toros were frequently seen, though never again together in such a large number.

Toros usually swim in groups of four to 10 individuals. Like roosterfish, they range rather freely up and down the shore, although individuals recognized by natural marks were seen repeatedly in the same vicinity over periods of at least several weeks at a time, and the species is more abundantly represented in some areas than in others.

Like roosterfish, toros appear with great frequency around the schools of *Selar*, *Microlepidotus*, and *Lythrulon* at Buena Vista. Also like roosterfish, toros often remain in the immediate vicinity of the schools throughout the day, where their behavior, as well as that elicited in the schooling prey, is as described above for *N. pectoralis*. Here too, the incidence of attacks is low during most of the day, although an attack was readily induced when one of the prey fishes was injured and unable to maintain its normal station in the school.

Toros, like roosterfish, increase intensity of predation early and late in the day, and here too the attack involves an explosive

FIGURE 25.—Toros, *Caranx hippos caninus*, patrolling in the vicinity of schooling prey.

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rush where it seems that the carangid is attempting to run down its prey. On three different evenings during mid-May 1964, I used SCUBA to sit on the bottom in the middle of a school of *Microlepidotus inornatus*, where I recorded the events during evening twilight. The sequence of events was essentially identical on all three occations. The following account, quoted from my field notebook, describes the activity on one of these evenings.

> Shortly after sunset the predators in the area, notably toros, increased the intensity of their predation. At the same time, the grunts also became more active—dashing first in one direction, and then in another. These abrupt evasive maneuvers, as well as the explosive rushes of the predators, became quite audible. The sharp snap of closing jaws at this time provided a rough index of increasing predation. Turbulence resulting from the increasing activity swept sediment up from the bottom, clouding the water which had been clear earlier, so that visibility became drastically reduced. The intensity of the activity, now heard and felt more than seen in the growing darkness, continued to increase until approximately 20 minutes after sunset. Then, suddenly, all was quiet. Although nothing was visible in the dark, turbid water, I had the distinct impression that all the fishes had moved away from me. However, in switching on my light I could see that I was still surrounded by grunts. Although the grunts about me scattered whenever I switched on the light, its intermittent use enabled me to grasp the situation.
>
> There was no longer any sign of the predators. The school of grunts had dispersed considerably and its members, having calmed down, were now swimming slowly, closer to the bottom. After a bit of oscillation, the grunts began a continuous movement offshore. Soon smaller grunts were passing me, probably members of schools which had been located inshore; then there was no sign of life. The sediment settled and except for a few scattered, smaller grunts and other fishes foraging over the sand, the bottom was empty. It was now approximately 25 minutes after sunset.

When feeding, toros show a series of distinct but relatively faint vertical bars on their sides.

I have observed toros attack flatiron herring at the water's edge, but even less frequently than roosterfish. On two occasions I saw toros thrashing about in the shallows, attempting to regain deeper water after stranding on the rocks while charging through a herring school. Occasionally, however, I observed toros feeding heavily on herring away from the beach.

Conclusion

The toro is a crepuscular predator, at least when preying on the schools of fishes near shore. Most activity is centered around schools of grunts and scads in 3 to 4 m. of water.

LUTJANIDAE

Lutjanus novemfasciatus Gill: Pacific dog-snapper (fig. 26)

Estimated period of direct observations: 11 hours.

Estimated period of general observations: 700 hours.

This is the largest of the lutjanids in the study area, often exceeding 1,000 mm. These large snappers were present on all the inshore rocky areas throughout the study. They are most abundant where large boulders and rocky shelves provide the caves in which they generally rest during the day, and from which they emerge during twilight. Although they feed to a large extent on schooling fishes, many aspects of their behavior are distinct from feeding habits of most other large piscivores.

When flatiron herring were present and being preyed on by most of the other predators, this snapper was conspicuously absent, even when it was known to be present in the area. Nor did I see this predator under schools of *Microlepidotus*, *Lythrulon*, *Selar*, and other schooling fishes in anything approaching the frequency of the other large piscivores. This may reflect their habit of retiring into caves during the day, rather than a real difference in activity, for all the large piscivores are relatively inactive during most of the day.

FIGURE 26.—*Lutjanus novemfasciatus.*

Fifteen specimens, 293 to 1,100 mm. long, were speared at different times of the day for food-habit study. No definite trends were evident in the degree of digestion undergone by the various prey, except it was apparent that little if any prey is captured during the day. This predator does much of its feeding after dark, and its food habits seem to be more diverse than those of the other large piscivores. Nevertheless, four of five identifiable prey fishes among the stomach contents were members of the schooling species, indicating that these prey are important food for this snapper too.

Although fishes are predominant in its diet, one 889 mm. specimen had ingested a spiny lobster, *Panulirus* sp., which had a carapace length of 89 mm. The lobster was in an advanced stage of digestion when it was removed from the snapper's stomach at 1130. Spiny lobsters range some distance from cover to feed at night, but they retreat into crevices among the rocks before first light, where they usually remain during the day. I doubt whether a large snapper could capture one after it has taken shelter and suspect that it was taken while active in the open during the night. The stomach of a specimen 1,100 mm. long, taken at the same time of day, contained the bones of a parrotfish, *Scarus* sp., approximately 450 mm. long. The parrotfish had probably been captured during the previous night, because its flesh had passed into the snapper's intestine by this time. Parrotfishes rest on the bottom in darkness, usually under rocky shelter, but some times in semiexposed locations.

When a predator feeds on a variety of prey differing widely in size, as does *L. novemfasciatus*, it is difficult to obtain a clear picture of digestion time. My data are

unsatisfactory on this point in regard to *L. novemfasciatus*. Longley (1923) conducted experiments on rate of digestion in *Lutjanus griseus* and found that fishes had passed the point where they could be identified 3.5 hours after ingestion. In the same study some crustaceans were also advanced in digestion at this time, while others remained largely intact.

Conclusion

This snapper feeds during twilight, and also shows evidence of extensive nocturnal activity. It takes a greater variety of prey as an adult than the other large piscivores, although schooling fishes still represent the greater part of its diet. It is largely inactive during most of the day, usually in caves.

Remarks on Other Large Piscivores

Other large predators also variably occur around the schooling prey species during the day. At Punta Pescadero the large serranids *Mycteroperca jordani* and *Epinephelus itajara* frequently move in under large schools of *Haemulon sexfasciatum* and *Lutjanus argentiventris* at dawn and dusk. These large predators, the latter occasionally exceeding 300 kg. in weight, are not present around the schools during midday. Sometimes they retire to caves in the immediate area, but usually they move out into deeper water, where *M. jordani* occurs during the day in groups of 10 to 15 individuals at depths of around 30 m. I have not seen these predators attacking the schools, nor have I examined their stomach contents. *E. itajara*, unlike most large groupers, is reported to feed mostly on crustaceans in the Atlantic (Smith, 1961). The amberjack, *Seriola colburni*, occurs occasionally around the schools of *Microlepidotus*, *Lythrulon*, and *Selar* at Buena Vista. Occasionally grey sharks, *Carcharhinus* sp., attack the schooling fishes in the bay at dawn and dusk, but I have not observed them thus engaged at other times of day.

While predation on the schooling species is largely crepuscular, I did not find strong evidence similarly linking predation on nonschooling fishes to twilight. No matter what the characteristics of the prey, there was generally little predatory activity during midday.

Summaries of Characteristics

NOCTURNAL SPECIES

All strictly predators. Relatively little diversity in feeding habits and structures. Most prey are small motile invertebrates, particularly crustaceans.

Two major groups:

I. Those schooling inshore during the day:

Two patterns of activity:

A. Most feeding among rocks or inshore near diurnal schooling sites. All bottom feeders. Prey relatively varied. Variable daytime feeding by individuals separated from their large diurnal schools, all active near rocks or close to the beach. Includes *Haemulon sexfasciatum*, *Anisotremus interruptus*, *Lutjanus argentiventris*, *Mulloidichthys dentatus*, *Umbrina xanti*.

B. Most feeding offshore, primarily in midwater, but some bottom feeding. All members of a school may feed largely on a single prey species during a

given feeding period. Do not feed during the day, and individuals generally do not leave the diurnal school. Includes *Harengula thrissina*, *Selar crumenophthalmus*, *Caranx marginatus* (juvenile), *Selene brevoorti*, *Microlepidotus inornatus*, *Lythrulon flaviguttatum*, *Orthostoechus maculicauda*, *Xenichthys xanti*.

II. Those secreting themselves under rocky cover during the day:
Two patterns of activity:

A. Feed on benthic organisms among rocks, do not move far over open bottom. Solitary when active. Prey relatively varied. Includes *Holocentrus suborbitalis*, *Epinephelus labriformis*, *Alphestes multiguttatus*, *Rypticus bicolor*. *Pareques viola*.

B. Feed in midwater aggregations on plankton. Aggregations move farther from cover and become more dispersed on darker nights. Prey relatively varied. Solitary during variable benthic feeding among the rocks. Includes *Myripristis leiognathus*, *Apogon retrosella*.

DIURNAL SPECIES

I. Activity on rocky bottom: Includes almost all diurnally active fishes considered in this study. Species grade from strictly predaceous, through a varying utilization of algae to strictly herbivorous (herbivores not considered here). Wide variety of feeding habits and structures. Most species take wide variety of prey, but some are highly specialized. Numerous patterns of activity; difficult to categorize:

A. Largely piscivorous: Stalk prey or rush from cover to capture proximate prey. Some, perhaps all, also variably active at night. Have more in common with some of the nocturnal predators than with other diurnal predators considered below. Includes *Fistularia petimba*, *Mycteroperca rosacea* (juvenile), *Epinephelus labriformis* (at night feeds largely on crustaceans).

B. Preying largely on invertebrates: No evidence of extensive nocturnal feeding.

1. Take individual prey from substrate. Do not feed regularly in midwater. Free swimmers. Includes *Bodianus diplotaenia* (adult), *Halichoeres nicholsi*, *H. dispilus*, *Pomacentrus rectifraenum*,[1] *Sufflamen verres*.
2. Pick individual prey from substrate. Variably feed in midwater. Variably engage in cleaning. Free swimmers. Includes *Heniochus nigrirostris*, *Bodianus diplotaenia* (juvenile), *Thalassoma lucasanum*.
3. Particulate feeder in midwater aggregations. Also feed on benthic material among rocks. Includes *Abudefduf troschellii*,[1] [2] *Chromis atrilobata*.
4. Sedentary predators feeding on or near bottom (not clear). Includes *Labrisomus xanti*, *Gobiosoma digueti*.[2]
5. Tube-dwelling predators that stalk or rush from cover to capture free swimming prey. Includes *Chaenopsis alepidota*, *Acanthemblemaria macrospilus*.
6. Free-swimming predators that feed on benthic organisms, with no apparent attempt to orient on individual prey. Includes *Gnathanodon speciosus*.

[1] Also feeds variably on algae.
[2] Also engages in cleaning.

C. Other:

1. Stalk or rush unseen to feed on mucous and possibly other dermal elements of larger fishes. Includes *Runula azalea.*

II. Activity over open sandy bottom: Relatively few species. All possess some adaptation to hide in sand. Both midwater and bottom feeders, all probably strictly predaceous. All inactive under sand at night. Includes *Hemipteronotus mundiceps*, *H. pavoninus*, *Taenioconger* sp.

Note.—Several prominent species diurnally active over open sand near beach are not covered in this study, e.g., gerrids.

CREPUSCULAR SPECIES

I. Feed largely on nocturnally active, diurnally schooling fishes:

A. Crepuscular feeding habits when preying on schooling fishes, with sharp peaks in feeding intensity during twilight:

1. From large inactive congregations in 3 to 6 m. of water during midday. Make increasing contact with prey between one hour before to 20 to 30 minutes after sunset. In morning, strong contact is maintained with prey from about 20 to 30 minutes before sunrise to 2 to 3 hours after sunrise.

a. Active in feeding groups of 2 to 10 individuals. Numbers within groups proximate to prey do not increase with more intensive feeding, but number of groups do. Includes *Elops affinis.*

b. Tend to aggregate with increased feeding activity. Numbers in aggregations increase along with intensity of feeding. Strong predilection for flatiron herring. Includes *Mycteroperca rosacea.*

2. Actively patrol inshore area in groups of 2 to 10 individuals during midday. Size of feeding groups proximate to prey do not increase with increased activity, but numbers of such groups do. Includes *Caranx hippos caninus*, *Nematistius pectoralis.*

B. Active during crepuscular period, but no distinct sharp peaks in feeding activity noted: Largely solitary as adult. Strong nocturnal habits apparent. Inactive, usually under rocky cover, during day. Includes *Lutjanus novemfasciatus.*

DISCUSSION

The work in Bahia de Palmas suggests several activity patterns within which the various fishes operate. Although segments of these patterns, as well as the relations of the patterns to one another, remain uncertain, a general picture can be drawn.

I have kept in mind the limited nature of the situation studied, and have guarded against overgeneralizing. The extent to which the generalities arrived at here apply to other situations awaits further work. The species considered were selected in part by the study methods. Many other species inhabiting this region were not studied, and these may or may not follow the activity patterns emerging from my data.

General Patterns of Activity

The large, relatively inactive schools of fishes over rocky bottom and along the shoreline are a striking element of the diurnal inshore community. These are nocturnally active fishes that feed on organisms becoming available after dark. Most of them migrate out over open sandy bottom offshore at night, an area largely devoid of diurnal activity, where they feed mostly in midwater. Others of these species do not migrate, but disperse in the vicinity of the diurnal schooling sites to forage on benthic organisms. Members of schools that disperse to feed on benthic material inshore also variably feed during the day, whereas members of schools moving offshore are limited to nocturnal feeding.

Large piscivores find these schooling fishes a prime source of food, and often keep them under surveillance throughout the day. Intense predation on members of these schools is largely limited to early morning and late afternoon, with relatively brief peaks during morning and evening twilight. Much of the behavior in the large piscivores is associated with behavior in the schooling fishes.

Nocturnal activity among the rocks, other than that involving the diurnally schooling fishes noted above, involves small solitary predators feeding largely on a variety of benthic crustaceans, or small midwater aggregations of fish that feed on a variety of plankton, mostly crustaceans. These predators are largely inactive under rocky cover during the day.

Diurnal activity among the shore fishes is mostly confined to the rocky areas, where feeding habits vary far more during the day than at night. Specialized feeding habits, such as cleaning and the variable utilization of algae as food, are also widely developed among the diurnal species. Prey are taken in both midwater and benthic regions during the day.

The pattern of activity in these fishes strongly reflects the threat of predators that keep the diurnal schools under surveillance, as well as the availability of prey after dark. Most of these species migrate offshore at night to feed, but a considerable number forage among the rocks and over the sand inshore.

Nocturnally Active, Diurnally Schooling Fishes

DIURNALLY SCHOOLING FISHES FEEDING OFFSHORE AT NIGHT

The offshore migration

One of the more striking aspects of the transition period from the diurnal to the nocturnal situation for shore fishes in general involves the flood of fishes that spread out over the open sandy expanses offshore at nightfall. The vast majority of these had been schooling inshore during the day. Included are such species as *Harengula thrissina*, *Selar crumenophthalmus*, *Lythrulon flaviguttatum*, *Microlepidotus inornatus*, *Orthostoechus maculicauda*, and *Xenichthys xanti*. I do not know the offshore limit of the migrations. With most prey of these fishes being taken from midwater, many may continue out beyond the relatively shallow sand flats to forage over deep water. The submarine canyons in Bahia de Palmas offer depths exceeding 500 m. within 3 km. of the schooling sites (Shepard, 1964).

The exodus of fishes from the beach at night, transforming the areas of open sand offshore into centers of nocturnal activity, coincides with the appearance of nocturnal invertebrates. Although I have no quantitative measurements of the relative diurnal-nocturnal numbers of these prey organisms in exposed positions, they are

readily observed after dark. Many small creatures, such as crabs and shrimps, move over the bottom, and plankton is also abundant, especially on dark nights when the midwaters teem with minute crustaceans and other animals. Relatively little of this life is apparent during the day, when many of these organisms presumably lie quietly in the sand. In a number of locations small but exceedingly dense concentration of mysids hover close to the bottom during the day. I did not see them in these locations after dark, when they probably rise to become part of the rich nocturnal fauna in midwater. The coastal euphausiid *Nyctiphanes simplex* is abundant in the Gulf of California, where in deeper water it rises toward the surface at night after being in the depths during the day (Brinton, 1962). Its occurrence and behavior in shallower water are poorly known, although Steinbeck and Ricketts (1941) reported the waters inshore at Punta Marcial to be "soupy with them." I did not identify the species of mysids or euphausiids in stomach contents, referring to them collectively, along with other similar forms, as "small, shrimplike crustaceans."

A number of reports have described the general nocturnal appearance of invertebrates (Longley, 1927; Starck and Schroeder, 1965; Starck and Davis, 1966). In my earlier report on diurnal-nocturnal activity (Hobson, 1965a), I stressed the significance of nocturnal accessibility of invertebrates to activity in fishes. Starck and Davis (1966) reported a strikingly similar situation in the Florida Keys.

The extent of this resource is illustrated by the diet of many of the fishes dispersing over open sand offshore at night. Consider, for example, schools of *Lythrulon flaviguttatum* or *Harengula thrissina*. The former are often composed of thousands, the latter of millions, of individuals. When these multitudes return to shore in the morning, their stomachs are often largely full of a single species of minute invertebrate prey.

Importance of proximate feeding grounds

In pointing out what they consider to be basic fallacies in attempts by Odum and Odum (1955) to explain the disproportionately large amount of animal biomass in a coral reef community, Starck and Davis (1966) cite the failure of these authors to consider the fact that many "reef fishes" are nocturnal animals that move away from the reef to feed at night. Bardach (1959) suspected that an ecological study of a reef not taking into consideration the surrounding sandy areas might provide misleading results, owing to the nocturnal forays away from the reef by the many pomadasyids and lutjanids. The importance of surrounding sand flats and grass beds as nocturnal feeding grounds for pomadasyids and lutjanids was noted by Longley and Hildebrand (1941) and Randall (1963).

The extent to which the diurnally schooling element of the nocturnal fauna develops depends to a large extent on the proximity of suitable feeding grounds to the diurnal schooling areas. Starck and Davis (1966) called attention to the extensive "back reef" areas in the Florida Keys that provide foraging grounds for the dense schools of pomadasyids and other species that inhabit those reefs during the day. They speculated that the general paucity of these fishes in so many regions of the Caribbean, despite similar reefs, reflects an absence of suitable feeding grounds. Randall (1963) emphasized the importance of adjacent feeding grounds in selecting locations for artificial reefs.

In Bahia de Palmas, the occurrence of the many diurnal schools of nocturnally active species is probably closely related to the proximity of suitable foraging grounds over extensive open sand expanses, and perhaps over canyons offshore.

Indirectly, then, the presence of these feeding areas must have a strong influence on the presence of large piscivores, which feed so heavily on the schooling species.

DIURNALLY SCHOOLING FISHES FEEDING INSHORE AT NIGHT

The diurnally schooling fishes that forage largely among the rocks or close to the beach at night are all bottom feeders. Included here are such species as *Haemulon sexfasciatum*, *Anistotremus interruptus*, *Lutjanus argentiventris*, and *Mulloidichthys dentatus*. The greater variability in their diet, as compared with the diet of species feeding over open bottom offshore, may be related to the greater complexity of the rocky habitat.

The rocky-bottom feeders are variably active during daylight, when some individuals and small groups leave the large diurnal schools to forage among the rocks. In contrast, the offshore feeders are not active during daylight, nor do they regularly leave their diurnal schools. The reason for this distinction in behavior remains unclear, although those active during the day readily excavate buried prey, an ability that is not developed in the offshore feeders. This ability, along with the continued proximity of cover during activity among the rocks, may contribute to the difference in diurnal behavior between the two groups.

CONSTANCY OF SCHOOLING SITES

During the day each of the nocturnally active, diurnally schooling species in Bahia de Palmas tends to school in a specific area. Thus *Selar crumenophthalmus*, *Lythrulon flaviguttatum*, and *Microlepidotus inornatus* school in a certain location at Buena Vista, but rarely elsewhere in the bay. Some species, such as *Orthostoechus maculicauda* and *Umbrina xanti*, although irregular in occurrence, consistently school in the same areas when they do appear. Even *Harengula thrissina*, which occurs intermittently at a number of different locations, seems to show an affinity for particular areas, although the situation here is more complex, and data are lacking. I found *Haemulon sexfasciatum* schooling within 30 m. of a particular large rock off Buena Vista point, frequently in a mixed group with *Mulloidichthys dentatus*, on every one of 143 daylight visits I made to that area.

A rough correlation exists between the size of the fish and the depth of water in which they school. This holds not only for different-sized individuals of the same species, but also for species of different size. Thus, not only do the smaller individuals of *Lythrulon flaviguttatum* school in shallower water than the larger ones, with juveniles occuring at the water's edge, but also the small-sized *Xenichythys xanti* schools in shallower water than does the larger *L. flaviguttatum*. The smaller juveniles of *Caranx marginatus* school at the water's edge, whereas the larger juveniles school farther offshore. This relation between size and depth holds from the largest of these schooling species, *Selene brevoorti*, to the smallest, *Harengula thrissina*. The relation breaks down in one respect, in that the larger herring (longer than about 50 mm.) school at the water's edge, whereas smaller individuals usually occur farther offshore. I will discuss this apparent inconsistency below.

Although my data on local patterns of distribution of the various schools is fragmentary, I believe additional study will establish the fact that a rather well-defined pattern does exist.

CONSTANCY OF INDIVIDUALS COMPRISING THE SCHOOLS

I cannot say with certainty that the schools are always composed of the same

individuals, particularly as these fishes often range far afield while foraging at night. I did not attempt any tagging, but some individuals that I was able to recognize by natural markings were in schools at the same locations day after day. Parr (1927) believed that when several schools of a particular species inhabit a region, their members become mixed after dispersing at night, so that the schools reforming in the morning are random samples of this mixture. In tagging programs carried out in the tropical Atlantic (Bardach, 1958; Randall, 1961; Springer and McErlean, 1962), members of species that move away from their diurnal schooling areas at night, for example *Haemulon sciurus* (Starck and Davis, 1966), were consistently recaptured or observed at the same locations on the reef over an extended period of time, indicating that such fishes return to a particular area after their nocturnal forays. Cummings et al. (1967), using underwater television to observe a school of *Haemulon album* in the tropical Atlantic, recognized several individuals that reappeared before the camera each day after the school had dispersed the previous night. They concluded that the school was formed day after day by the same fish that reappeared in the same location each morning.

My observations strongly indicate that, though variably dispersed, many members of at least some diurnal schools, for example *Microlepidotus inornatus*, maintain contact with one another at night, and at least much of the school may continue to operate as a unit during nocturnal forays. The grunts moving out over open sand are not randomly scattered, but rather occur in localized concentrations. Fishes active in midwater out over open bottom do not operate as individuals in nearly the frequency of fishes that are active among the rocks inshore.

NOCTURNAL FEEDING AND THE DISPERSAL OF SCHOOLS

Some authors, for example Morrow (1948), in stressing the role of vision in schooling, have suggested that schools disperse at night because schooling fishes are unable to maintain visual contact in darkness. Species studied here offer no support for this theory. It was always my distinct impression that these fishes disperse because the large, dense schools formed in daylight are incompatible with nocturnal activity. The term "disperse" is used here in a relative sense to contrast the nocturnal and diurnal groupings. The many species discussed above, though separated in loose feeding aggregations and as individuals at night, nevertheless seemed quite capable of maintaining contact with one another.

Many authors have investigated the effect of darkness on fish schools. Breder (1959) stated: "The dispersion of schools in darkness has been so often reported that it is to be expected unless otherwise shown." Loukashkin and Grant (1959) reviewed the literature which reports dispersal of schools at night and establishes vision as the dominant sensory modality involved in integrating and maintaining schools and aggregations. Moulton (1960), noting that *Anchoviella choerostoma* and *Clupea harengus*, among others, maintain their schools at night, considered the possibility that swimming sounds enable these and other fishes to school in darkness. Keenleyside (1955) suggested that *Scardinius erythrophthalmus* may maintain its schools at night through specific olfactory stimulation, and speculated on the possibility that a wide range of senses may function to keep fishes together in darkness. Hemmings (1966) felt that olfactory cues keep schooling fish together at night. Schools of *Microlepidotus inornatus*, and other pomadasyids, give evidence of

continuing to operate as a unit after dispersing offshore after dark. The well-developed ability of these fishes to vocalize may be important in maintaining the integrity of the nocturnal groups.

As Shaw (1961) pointed out, much of the controversy stems not from whether or not fishes school at night, but rather what the various authors mean by night, in terms of the level of incident light available to the fish. It is certainly unrealistic to equate night with complete darkness when dealing with shallow water or pelagic surface fishes. Whether from moon, stars, or luminescent organisms, some light is usually available. While diving in clear water at night, I have been able to distinguish fishes in the water above me, using the surface as a contrasting background, when the only source of illumination is starlight. Furthermore, in many areas of the sea at night a moving object is readily observed owing to the luminescence of many minute planktonic organisms that light up when disturbed. I discussed these and other points in an earlier paper (Hobson, 1966) that considered possibilities of nocturnal foraging in pinnipeds. Some small midwater crustaceans, for example *Nyctiphanes simplex*, possess well-developed photophores that may serve as visual targets for nocturnal predators. As noted above, this particular euphausiid abounds inshore in the Gulf of California.

Thus nocturnal creatures, specialized to the task, should find ample means of orienting visually at least much of the time at night. A number of authors have shown little awareness of the range of potential visual cues that exist under the sea after dark. For example, Nikolski (1963) thus accounted for the dispersal of schools: "Since shoaling fishes mainly sense the presence of predators visually, the shoal cannot have any protective significance against predators which feed at night." Similarly, Manteifel and Radakov (1961) assumed that nocturnal predators do not hunt visually when they stated that "the shoaling of 'seeing' fish . . . is inadaptive and harmful when they are attacked in the dark by nocturnal predators. This is probably why shoals of these fish break up . . . at dusk for the night." These authors greatly underestimate the extent to which vision can be used at night by both predators and prey. If, as Longley (1917) and others have suggested, countershading effectively aids in concealing midwater fishes from predators and prey, the nocturnal color pattern of *Myripristis leiognathus*, described in this report, may imply not only the threat of a visually feeding nocturnal predator, or visually alert prey, but also the presence of a significant amount of light from above at night.

In any event, when an investigator subjects his fish to total darkness in the laboratory, he has usually created an atypical nocturnal situation. Kavanau (1967), working with rodents, also stressed this fact in regard to the terrestrial situation. A number of studies have attempted to measure the level of incident light at which fish schools disperse (Ali, 1959; John, 1964; Loukashkin and Grant, 1959). Although many of the fishes studied were found to be capable of schooling under light equivalent in intensity to moonlight, Ali found that *Oncorhynchus* can school with no more light than that made available by the stars. The different results obtained by various authors may be due to species differences, but Shaw (1961) found disparity in experimental procedures and semantic inconsistencies which she felt could have contributed much of the variance.

When comparing observations of the dispersal of fish schools in aquariums with the situation observed at sea, one must keep in mind the limited space available to

fishes in tanks. Even when fishes in captivity disperse at night to the point where they are spread throughout the limited area within their tanks, one should not assume from this that in the sea they will continue this dispersal until all semblance of a group is lost. Often, at least, the observed dispersal may merely reflect the transition to such loosely spaced nocturnal feeding groups as I have been describing.

Considering that most diurnal-nocturnal transitions in behavior occur during twilight, it is astonishing that little concern has been given in laboratory work to this critical period. Investigations dealing with such phenomena as the dispersal of the fish school under diminished light intensity are subject to serious question if an accurately simulated twilight period is not part of the program. Kavanau (1967) discussed the importance of twilight to experimental programs in the laboratory, and Olla et al. (1967) took twilight into consideration in designing the experimental tank for the U.S. Bureau of Sport Fisheries and Wildlife Laboratory at Sandy Hook, N.J.

In my opinion, proper consideration has not been given to activity normally engaged in by the various species during day and night. What does the onset of darkness mean to the species in question? We have seen that, to the many diurnally schooling fishes considered here, darkness is a time to feed, and they disperse from their large, inactive, diurnal schools to forage. Yet if an inability to maintain contact with one another is the basis for this dispersal, one can hardly account for the loosely spaced feeding aggregations in which most of the fishes operate at night. Maintaining contact at night in these relatively widely spaced, active associations seems to present a greater sensory challenge than would be the case if they had retained the relatively close spacing of their inactive diurnal schools. Consider, too, the nature of prey sought at night. There is no good evidence that vision is not the major sensory modality used by at least most of these fishes in capturing the minute plankton that is so much of their food. To the contrary, the enlarged eyes of so many nocturnal species, such as *Selar crumenophthalmus*, strongly suggest that vision is widely used after dark. Starck and Davis (1966) certainly suggested that vision is important to nocturnal fishes when, in drawing a general distinction between diurnal and nocturnal species, they stated that "eyes of diurnal species . . . tend to be smaller than those of nocturnal species." The ability of so many diurnally schooling fishes to hunt minute prey at night seems incompatible with the idea that schools disperse with darkness because their members are no longer able to maintain visual contact.

Work by Steven (1959) with *Hepsitia stipes* in aquariums is pertinent. He described an "alarm reaction" in these fish after exposing them to an extract of skin from other members of the same species. Significantly, he found the response especially marked at night after the fish had dispersed from their diurnal school and were scattered throughout the aquariums. Upon introduction of the extract into the aquariums in darkness, the fish immediately formed a tight school. Similarly, Thines and Vanderbussche (1966) found that *Rasbora heteromorpha*, in an aquarium, schooled in darkness when an alarm substance was introduced. They found the effect more pronounced with fish held in darkness during daytime than in those held in darkness during night, and postulated a diurnal fluctuation in readiness of fishes to school in response to external stimuli.

The Large Piscivores

RELATIONS WITH NOCTURNALLY ACTIVE, DIURNALLY SCHOOLING FISHES

Primary prey of all the large piscivores in Bahia de Palmas are nocturnally active fishes that school inshore during the day. Although I have no quantitative data, I am confident that these fishes represent the largest source of appropriate-sized prey in the area for large piscivores. By appropriate-sized I mean not too large to be efficiently manipulated by the predators and yet large enough that food ingested more than makes up for energy expended in making the capture. Their concentration in dense schools during the day, consistently in the same locations, probably makes their location well-known to predators. We have seen, however, that relatively little predation occurs through most of the period these schools are present inshore. Possible reasons why these prey species are, in fact, not as available as they might seem to be are presented below.

The predominant role of schooling fishes in the diet of larger piscivores is probably related to their relative abundance. Randall (1963) reported that *Mycteroperca*, *Lutjanus*, *Caranx*, *Seriola*, and other predators in the Virgin Islands, feed more heavily on parrotfishes than on any other group, noting at the same time that parrotfishes are the predominant family on those reefs. Conversely, Bardach (1959) found that parrotfishes are rarely the prey of Bermuda piscivores, which is the situation I encountered in the Gulf of California, where parrotfishes are not a major group. Considering the West Indian situation further, Randall (1963) speculated that pomadasyids would probably be the predominant prey on patch reefs, where these species are concentrated.

Behavior in the large piscivores in Bahia de Palmas is intimately associated with activity patterns in the schooling fishes. The interplay between predatory activity in *Mycteroperca rosacea* and behavior in *Harengula thrissina*, as described at length in this report, clearly illustrates the close tie in the activity of both species.

Relative availability of schooling fishes

Such predators as *Nematistius pectoralis* and *Caranx hippos caninus* keep the large schools of pomadasyids and other schooling species under diurnal surveillance. Nevertheless, in their diurnal schools these prey seem to be at least relatively safe from predation, as intensive exploitation of these schools is limited largely to periods of early morning and evening, with peaks during twilight. Yet the attending predators readily feed during midday when presented with the opportunity. This capacity is illustrated by the immediate reaction of these big fishes to prey that are no longer able to maintain their station in the school because of injuries.

The manner in which predators may swim among schooling prey for long periods of time during the greater part of the day without attempting to feed suggests that, during these periods, the predators do not regard the schooling fishes as available prey. I believe that the element(s) of the school responsible for this effect experiences periodic lapses during which at least some of the schooling fishes are vulnerable, and which are sensed by the predators through cues that trigger attack. In this manner, predators do not expend energy without a certain degree of chance for success.

The large piscivores most certainly exhibit appetitive behavior when slowly patrolling through the schooling areas, with attack awaiting only an appropriate stimulus. The exact nature of the stimulus

remains unclear, but during the day often seems to be associated with disorientation of segments of the school, or isolation of one or a few of its members. Attacks on isolated members of schools were noted in this report, and have been widely reported elsewhere (Eibl-Eibesfeldt, 1962; Hiatt and Brock, 1948; Starck and Davis, 1966). Hiatt and Brock observed three skipjacks *Euthynnus yaito* closely escorting a school of scad *Decapterus sanctaehelenae* over a coral head rising from deep water in a Marshall Island lagoon. Although they observed this activity over a 3-hour period, only once did the tuna attack, and this one effort was directed at a solitary scad that had become separated from the school.

Observations by Eibl-Eibesfeldt (1962), as well as by Starck and Davis (1966), further demonstrate the vulnerability of an isolated individual, and also suggest that predators may not always wait for schooling fishes to become available, but may themselves take action that creates the proper situation. Eibl-Eibesfeldt described the manner in which *Caranx ascensionis* in the Indian Ocean drives into tightly packed schools of *Caesio cuning*, a maneuver he felt separates individuals from the group. Similarly, Starck and Davis observed *Caranx bartholomaei* charging into schools of pomadasyids in the Florida Keys, and felt that these actions scatter the school, thus enabling the predators to attack individuals that have been isolated.

The vulnerability of disoriented or disorganized segments of schools was illustrated by accounts of several incidents in this report. Phillips (1952) noted that a disorganized group of sardines *Sardinops sagax* was quickly consumed by mackerel *Scomber japonicus* at sea off California. On the other hand, he was impressed by the relative security enjoyed by sardines and anchovies in schools under attack by mackerel and barracuda.

It remains uncertain why the large piscivores find schooling species increasingly available during twilight. Nevertheless, during the transition period between the diurnal and nocturnal situations, it appears there is a relative breakdown in whatever may be the mechanisms that protect schooling fishes during most of the day, and the piscivores seem to find them particularly vulnerable. Not only do the vigorous open assaults of the large carangids apparently attain maximum effectiveness, but various modes of attack in other predators are also employed with increased frequency.

In a report dealing primarily with feeding in pinnipeds (Hobson, 1966), I suggested a possible reason why crepuscular habits are advantageous to *Mycteroperca rosacea* and other predators that characteristically attack from below. Despite the fact that the sky itself is relatively light for some time after the sun falls below the horizon in the evening, and just before its rising in the morning, little of this light penetrates the water, and from a position in midwater a predator below is difficult to distinguish. From below, the prey in the water above stand out sharply against the light surface. I have found fishes silhouetted above me to be actually far more apparent than when they are viewed from this same position during midday.

Intense predation was often traced to confusion or disorientation developing for a variety of reasons among the ranks of schools migrating away from shore in the evening. The accounts of incidents involving flatiron herring at the rock-sand interface of Punta Soledad are examples.

Despite what seems an increased vulnerability of schooling fishes during twilight, the schooling habit apparently continues to be at least relatively advantageous during this period. Where observations permitted examination of the question, the fishes remained in their schools until after the period of intense

predation in piscivores had passed. For example, *Microlepidotus inornatus* did not disperse from its school at Buena Vista until after *Caranx hippos caninus* and other large piscivores had withdrawn.

One is led to the conclusion that piscivorous activity is intimately related to school formation in prey. My observations indicate that school formation provides a degree of protection from predation. The effectiveness of the school in providing protection appears to fluctuate, and this fact strongly influences behavior in predators. The effectiveness of the school seems to be minimal during the transition period between diurnal and nocturnal situations, that is, during twilight, thus accounting for intense predation at this time.

Role of the School in Predation

ROLE OF THE SCHOOL IN REDUCING PREDATION

It is widely believed that school formation reduces predation on the schooling species, but there is considerable disagreement about the mechanism(s) involved. At least some of the controversy may arise from the possibility that under varying circumstances different mechanisms are in effect. This point must be kept in mind when considering the different theories in light of my observations in a limited situation.

Some theories

Breder (1948), Springer (1957), and others have speculated that predation on some schooling fishes may be deterred through what has been referred to as "collective mimicry." It is suggested that fishes in a group may appear to the predator as some larger inedible or even threatening object. I found no support for this view. One would expect such a phenomenon to be most marked when visibility is reduced, as during twilight. Quite to the contrary, schooling fishes are most heavily exploited at this time.

Brock and Riffenburgh (1960) approached the problem theoretically. They assumed that a predator feeds to capacity upon sighting a school, and yet concluded that the school functions to reduce predation through a combination of the predator's food capacity limitations on any one occasion and a reduced number of predator-prey encounters. These authors clearly had an offshore habitat in mind, as their assumptions and conclusions are unrealistic in regard to the inshore situation considered here, where the same predators are feeding on fishes from the same schools in the same locations day after day.

Williams (1964) believed that schooling is an expression of cover seeking, through which a fish in the center of a school is protected by the presence of many other individuals between itself and the predator. That any advantage obtained by a fish sheltered in this manner would be at the expense of other individuals of the same species at the school's periphery did not seem to concern Williams, but would certainly negate any advantage such a maneuver would have to the species.

Bowen (1931) suggested that schooling in juveniles of *Ameiurus melas* is advantageous because "the many eyes of the group compensate for the rather poorly developed eyes of the individual. The sudden movement of one fish induces movement among all the members of the group." Eibl-Eibesfeldt (1962) and others have pointed out that schooling fishes in general may enjoy an increased ability to sense a potentially dangerous situation through the increased number of sensory receptors in the group. Considering the highly developed sensitivity of schooling fishes to the actions of any segment of the

school, or "group cohesion," as discussed by Welty (1934), added security may be obtained through an increased number of individuals. However, this interaction among schooling fishes may, to the contrary, have a negative effect by actually retarding the evasive response of the first individuals to sense danger. Inasmuch as these individuals quite likely would be among those to which the danger is most imminent, this possibility must be considered.

The confusion effect theory

Laboratory experiments have shown a decrease in prey consumption with an increase in prey concentration. Welty (1934) observed this effect when using goldfish *Carassius auratus* as predator and *Daphnia* as prey. He attributed this effect to confusion arising in a predator confronted with many alternative stimuli presented by the multiple prey. Similar results were obtained by D. V. Radakov using coalfish *Pollachius virens* as prey and cod *Gadus morhua* as the predator (Nikolsky, 1963).

A number of studies have favored a "confusion effect" as being an important factor in the school's role in reducing predation (Allen, 1920a, 1920b; Eibl-Eibesfeldt, 1962; Manteifel and Radakov, 1961; Hobson, 1965a; Starck and Davis, 1966). The fact that a recent article dealing with the significance of schooling (Iversen, 1967) does not even mention this theory indicates that it has not gained wide acceptance. The theory contends that a predator required to direct its attack at an individual fish experiences difficulty when confronted with the numerous targets presented by a school, finding members of the school difficult to distinguish. This theory is generally consistent with my observations. Fishes that do not select individual prey, such as anchovies and others that passively filter small organisms from the water, would not be affected. However, I am not considering such predators in this report.

Breder (1959) expressed doubt whether a confusion factor is in effect when *Caranx* attacks a school of *Sardinella*, and when *Sphyraena* strikes into a school of *Jenkinsia*. This doubt was based primarily on his failure to observe hesitancy or indecision in the feeding strikes of these predators. If confusion does enter into these situations, I would not expect it to be evident to a human observer. That slight changes in conditions profoundly affect attacks of predators on schooling fishes suggests that a fine line exists between success and failure of attacks.

The tightening of schools under threat of attack

If, as the confusion effect theory suggests, a predator is confused by multiple targets, then the more of such targets that can be placed in the predator's visual field, the greater should be the effect. The manner in which schooling fishes tighten up their schools when threatened is consistent with this aspect of the theory. Schools of fishes considered here frequently responded to the approach of a predator in such a manner, and similar accounts are widespread (Allen, 1920a, 1920b; Blaxter and Parrish, 1958; Breder and Halpern, 1946; Eibl-Eibesfeldt, 1962). As a predator rushes into a school, the tightly packed members then radiate out in all directions before the advancing predator, probably contributing to any confusion effect that might be operating. Baerends and Baerends-Van Roon (1950) felt that a rapid change in density of the school, in itself, confuses the predator, whereas Bowen (1931) felt that rapid scattering of schooling *Ameiurus* made it impossible for the predator to keep one individual in view.

On the other hand, some investigators (e.g., Kishinouye, 1923) have interpreted the tightening up of prey schools when threatened as being the result of "herding" maneuvers by predators that function to

the benefit of the predator in producing the crowding effect. This line of thought suggests that prey fishes are in fact increasingly vulnerable to predation when in tight schools. Williams (1964) noted that predation is likely facilitated in some situations when prey form a school. Bullis (1961) described situations where schooling in prey seemed to make them more vulnerable to predation, especially when drawing themselves close together. In one instance, he described a whitetip shark, *Carcharhinus longimanus*, feeding on a "dense ball" of threadfins, *Polydactulus* sp., "biting off mouthfuls of fish, much in the manner of a person eating an apple." He also noted that "apparently the school of threadfins was completely indifferent to the predation." At least part of the disagreement may stem from the distinct possibility that some predators, not seen by me, have developed methods of attack that capitalize on what is generally an advantageous defensive maneuver of the prey, and, in fact, do feed most readily on tightly schooling prey. The specialized feeding behavior reported by Nichols and Murphy (1916) in the thresher shark, *Alopias vulpinus*, may be another example.

Other possible means of masking the individual in a school

The schooling fishes in Bahia de Palmas not only draw themselves closer together when threatened, but also increase swimming speed as individuals begin to weave in and out about one another. Such behavior is certainly effective in making the individual more difficult to distinguish. In my own attempts to spear these fish for stomach-content analysis, I experienced difficulty following an individual under such conditions, and in order to achieve any degree of success with the spear it was necessary to aim at individuals. In collecting *Selar crumenophthalmus*, for example, I could occasionally spear fish by firing blindly into the tightly packed school confronting me. Usually, however, such an effort would find my shaft sailing harmlessly through a void that suddenly materialized in the school along the path of the spear. In order to collect these fish effectively, I found it necessary to take aim on an individual—a relatively difficult task when the scad were alerted.

The effect of masking the individual is greatly enhanced when the schooling fish is silvery, like *Harengula thrissina*. When such fishes are alerted, they, like the other schooling species, increase their swimming speed as they begin to dart in and out. Because of the irregular, constantly changing course they follow, sunlight reflecting from their silvery bodies at rapidly changing angles is manifested in a large school as a bewildering shower of brilliant flashes. B. W. Walker, of the University of California (personal communication), suggests that a predator may fix its attack on the position of one of these intermittent flashes, thus invariably missing the herring, which has since moved on. Breder (1959) cited the high incidence of silvery fishes among schooling species and speculated that the flashing sides, visible at a distance, might function in reestablishing the school after a dark night. While noting that such silver flashes are produced as these fishes make turning movements, he stressed his belief that in their normal quiet swimming, the mirrorlike sides of silvery fishes reflect their surroundings and thus blend into the background. Denton and Nicol (1965), following a histological examination of the structures involved in reflection of light by *Clupea harengus*, presented extensive theoretical evidence to account for "the invisibility conferred upon it by its silvery sides." These two possible functions of silvery sides in so many schooling fishes are not necessarily mutually exclusive. As Breder suggested, the characteristic which enables a silvery fish to blend with its surroundings may

function in a quiet, undisturbed school. The profusion of flashes produced by alerted herring, as described above, may then come into play when the school is attacked. But at any given moment in even the quietest of large schools, some individuals are turning on their sides to the extent that flashes of light are emitted. Nevertheless, the aspect of these quiet schools is one of inconspicuousness.

Anchovetas, *Cetengraulis mysticetus*, often swim in well-defined subschools among flatiron herring. Although I never saw them comprise more than 10 percent of the entire school, the anchovetas were preyed on by gafftopsail pompano, *Trachinotus rhodopus*, far more heavily than were the more numerous flatiron herring of similar size surrounding them (Hobson, 1963c). These anchovetas are filter-feeders, swimming with gill covers widely distended even while in dense schools during the day. In this distended position, the gill covers reflect sunlight, and it was suggested that these reflections may serve as lures to draw the attention of the pompano, hence explaining why they were selected over the herring in numbers highly disproportionate to their relative numbers in the school. Reflections from the rigid gill covers of the anchovetas are not flashes, like those produced by alerted herring, but rather discrete points of light. There would be no confusion produced on a predator here, as the continuous reflections would have more the effect of distinguishing than of masking the individual. The cluster of steady lights manifested by the subschool of anchovetas among the more numerous, but far less apparent herring, would seem readily accountable for attracting the attention of predators, and perhaps even directing their attack.

It is also characteristic of schooling fishes that all members of a particular group tend to be of about the same size, as well as being of similar external appearance. Schooling fishes are noted for lacking noticeable external sexual differences. These factors further contribute to masking the individual, as dissimilar members would be readily picked out of the group. W. A. Starck II (personal communication) found that fishes he had marked with fluorescent dye in hopes of mapping their movements after dark were quickly taken by predators after they had returned to their schools, even though he felt that the marked fish were behaving naturally and holding a normal station in the school. Starck (1966) also noted significance in the striped and barred color patterns of so many schooling species, pointing out that the "shifting maze of lines makes individuals difficult to distinguish."

Possible significance of water depth at schooling sites

The depth of water in which fishes of various sizes school in Bahia de Palmas may contribute to deterring some predators. The general return of the schooling fishes each day to relatively shallow water near shore is a striking phenomenon. Herring and juveniles of other species are the smallest, and most take up locations right at the water's edge. The larger individuals school farther offshore, at increasing depths of water that roughly parallel an increase in fish size. The larger fishes tend to be in the deepest water. Although many factors probably contribute to this situation, such a distribution should have some effect in regulating the size and type of predators able to maneuver effectively at these locations.

The contention that confusion would involve predators having to orient their attacks on individuals suggests that the most striking examples may be found where predator-prey size differential is small. A predator feeding on prey relatively large in relation to its own size would be among those most likely required to take prey individually, and hence most affected by the

proposed confusion effect. It is possible that by schooling in shallow water a relatively low predator-prey size differential is maintained, and the proposed confusion effect factor thus held maximal.

Flatiron herring present an exception to the general size-depth relation. Individuals over about 50 mm. school at the water's edge during the day, but smaller herring generally school at the surface some distance away from the beach. This contrasting behavior may be due to a difference in food habits between the two size groups. It may also be that although larger herring are not exploitable by the numerous small benthic predators of comparable size that regularly inhabit shallow water, such as clinids and gobies, the smaller herring might be potential prey of these fishes and as such more secure away from the bottom in deeper water.

Larger individuals of *Mycteroperca rosacea* moving inshore beneath flatiron schools at dawn and dusk are well suited to feed on schooling prey in shallow water. Their ability to rest on the bottom under the school, and attack with a short explosive upward rush, would seem more effective in these surroundings than the space-consuming maneuvers of large carangids. Although large roosterfish and toros do attack the herring schools inshore, especially during early morning and evening, the relative difficulty they experience at such times is illustrated by the observations of several of these predators being stranded at the water's edge following a seemingly reckless charge through the herring. Similarly, Eibl-Eibesfeldt and Hass (1959) observed a shark, *Carcharhinus* sp., strand itself on a sandy beach after overshooting prey at the water's edge. It is therefore not surprising that the large carangids are far more active around schools of larger prey in deeper water.

It may be significant that prey schools normally located 20 to 50 m. offshore often move into very shallow water when under heavy predation. Occasionally, in their evasive maneuvers to elude predators, they too strand themselves on the beach. Eibl-Eibesfeldt (1962) suggested that predators gain an advantage when prey are thus driven into cramped quarters, and that maneuvers of the predators are effective because they create this situation.

Yet even should there be no means whereby fishes in schools can exert some control over the size of predators they encounter, studies like those of Welty (1934), who used goldfish and *Daphnia*, suggest that a confusion factor is in effect even where the predator-prey size differential is large, just so prey are taken visually, one by one.

COOPERATIVE FEEDING EFFORTS OF PREDATORS IN SCHOOLS

Sette (1950) regarded the school as an aid to predators in capturing prey, rather than to prey in avoiding predation. He noted that schooling mackerel *Scomber scombrus* are filter-feeders when preying on plankton, and at this time swim with mouths held wide open and operculums distended. Sette likened such a feeding school to a group of miniature tow nets, spaced closely together, and suggested that effectiveness of feeding is increased through schooling because as plankton dart aside to avoid one predator they put themselves in the path of another. Carrying his speculations further, Sette suggested that schooling predators enjoy the same advantage when they attack fishes. Predation by bluefish, *Pomatomus saltatrix*, on menhaden, *Brevoortia tyrannus*, was cited as an example. Sette stated that "a menhaden eluding one bluefish would be in the path of another, if the bluefish were in schools." An analogy to "miniature tow nets" presupposes that the predator need not direct its attack at an individual when feeding on members of a school.

Bullis and Juhl (1967) observed little tuna, *Euthynnus alletteratus*, feeding in a tight formation, with members maintaining physical contact with one another. These authors suggested that such a closely spaced formation might prevent prey from darting between the predators and escaping. Fink (1959) reported groups of porpoises *Phocaena vomerina*, spaced about 30 cm. apart in concentric formations, feeding effectively on a school of Pacific sardines, *Sardinops caerulea*.

The simultaneous attack by a number of predators might be advantageous, not so much because prey eluding one predator place themselves in the path of another, but more because the structure of the school has been disrupted at the point of attack. Prey disoriented by the attack of one predator may thus become vulnerable to attack by another. Above, I describe waves of disorientation radiating out through a herring school from points where pelicans had plummeted into the water, and note that a cabrilla struck at these disoriented segments of the school.

Cabrilla tend to aggregate under herring schools during periods of maximum predation. The simultaneous rush by all the members of these aggregations often brings the whole group erupting from the surface of the water together. The predators may gain some advantage through their numbers, but the mass rush may also be no more than an expression of the greater number of cabrilla operating under the herring during the more favorable feeding period.

Nevertheless, larger piscivores, such as carangids, generally operate in groups of two to six or more individuals, and it seems likely that they feed to advantage in numbers. In an incident referred to above, Eibl-Eibesfeldt (1962) felt that the activity of *Caranx*, in isolating members of a *Caesio* school, is a coordinated effort.

In another incident referred to above Hiatt and Brock (1948) described how three skipjacks "herded" a school of scad over an isolated coral head. They stated:

> Now and then the scads would turn off to one side, at which time the tuna on that side would move forward swiftly and herd them back into line. It became obvious that the school of scads was prevented from leaving the area over the top of the coral head, being herded back whenever it moved over deeper water.

The account implies that it was to the advantage of the skipjacks to keep the prey tightly schooled in relatively shallow water. Another interpretation of this activity is that the scad, in their dense school, occupied the most favorable position attainable for them under the circumstances, and were in fact relatively secure from the skipjacks as long as they remained there. This view gains support from the fact that the only attack Hiatt and Brock observed during a 3-hour period was directed at a straggler. Whenever a segment of the school turned toward deeper water, the skipjacks bolted toward it. Perhaps the predators sensed this segment as being in a more vulnerable position and reacted accordingly, with the immediate withdrawal of the scad being simply a return to a more secure position when threatened. If this interpretation of the activity is correct, then the term "herding" in reference to such activity in predators is misleading.

Manteifel and Radakov (1961) reported that prey fish, even when solitary, become disoriented when they are attacked by a group of predators and hence are more readily captured. These authors also noted the advantage of numbers when searching for prey, although this last consideration would offer little advantage in the situations discussed here, where prey are consistently in locations that must be well known to the predators.

Other Activity

THE MIDWATER AGGREGATORS

Although many of the schooling fishes discussed above move over considerable distances while making migrations to feeding grounds, another group of fishes, some diurnal, others nocturnal, show well-defined movements that are, however, restricted to distances of no more than a few meters. These are the many small plankton-feeders that rise into midwater from the sheltering bottom. Included here are such species as *Chromis atrilobata*, *Abudefduf troschelii*, and *Hemipteronotus mundiceps* among the diurnal forms, and *Myripristis leiognathus* and *Apogon retrosella* among the nocturnal forms.

Both diurnal and nocturnal fishes tend to form aggregations when moving away from the substrate. Nevertheless, members of the diurnal aggregations are generally more closely spaced, and their groups are usually better defined, than members of aggregations forming after dark. Furthermore, nocturnal aggregations tend to be increasingly dispersed on darker nights.

Planktonic crustaceans comprise the bulk of the diet of these fishes, particularly among the nocturnal species, but members of at least one diurnal species, *Abudefduf troschelii*, feed to a large extent on algae. That the formation of aggregations is associated with feeding in midwater is indicated by the fact that these same fishes are dispersed, and forage independently, when feeding on benthic organisms.

Activity in these fishes is largely concentrated over or around the spot where they find shelter during their inactive period. A diurnal species, like *Chromis atrilobata*, often shares a location about a large rock with a nocturnal species, like *Apogon retrosella*. The two species exchange positions during morning and evening twilight, frequently schooling together around the base of the rock as one species is emerging and the other is going under cover (Hobson, 1965a). Neither diurnal nor nocturnal species are in midwater during the latter part of evening twilight or the early part of morning twilight.

AGGREGATIONS, SCHOOLS, AND PREDATION

If schooling fishes do enjoy a degree of security from predators due to the nature of the school, as discussed above, one immediately wonders about other smaller species.

It is probably significant in this regard that the midwater plankton-feeders aggregate when they move away from cover. Furthermore, even small fishes generally active close to cover, for example *Thalassoma lucasanum* and *Halichoeres dispilus*, tend to aggregate whenever they move more than a few centimeters from the substrate.

Any benefit a school might obtain in minimizing predation from a proposed confusion effect, or most other suggested mechanisms, would be shared by members of these aggregations.

Several authors, including Keenleyside (1955) and Williams (1964), have in fact regarded these aggregations as schools. Keenleyside considered that "any fish aggregation can be considered a school provided the fish are together because they are reacting to each other and not because of similar reactions by each individual to a common external stimulus." At least in regard to a role in reducing predation, the associations I have referred to as aggregations probably function in the same way as those I have called schools.

Although all members of the midwater plankton-feeding aggregations are orienting on food, the groups themselves are

maintained by the fish remaining near one another. I base this contention on the fact that the aggregations form despite the fact that the planktonic food of these fishes is usually widespread throughout the area.

In obtaining protection from predators, fishes actively feeding in midwater aggregations would seem to suffer some disadvantages when compared with members of the diurnally inactive schools of such fishes as flatiron herring. For example, the spacing between individuals in the midwater feeding group, while variable, is relatively great (compare figs. 7 and 12), and the behavior of schools under attack has suggested that security increases with a decrease in space between individuals. Furthermore, any advantage small fishes might gain in forming their schools in shallow water would not be shared by the many small midwater plankton feeders offshore.

Both considerations are expressed in reactions to potential danger by members of the midwater plankton-feeding aggregations. In abruptly discontinuing feeding, and drawing themselves close together when threatened, they provide further evidence that such a close grouping does indeed increase security. Any advantage such smaller fishes as flatiron herring may gain by being in shallow water is probably offset in the smaller midwater plankton-feeding fishes offshore by the habit of the latter of diving under cover when threatened—an advantage not shared by the herring.

In regard to predation, the midwater plankton-feeding fishes, diurnal as well as nocturnal, may enjoy at least one big advantage over the relatively inactive schooling species. As noted above, during those periods of morning and evening twilight, when schooling fishes are most heavily exploited, neither diurnal nor nocturnal plankton-feeders are in midwater.

ACTIVITY NEAR THE BOTTOM

Nocturnal activity among the rocks

Feeding habits of fishes active among the rocks at night reflect an increase in availability of small invertebrates. Habits of the diurnally schooling species that disperse among the rocks at night are discussed above. Other predators feeding on the bottom, like *Rypticus bicolor*, *Alphestes multiguttatus*, and *Pareques viola*, feed largely on benthic crustaceans during their solitary nocturnal forays. Perhaps a better illustration of the increased availability of small crustaceans at night is offered by *Epinephelus labriformis*, which feeds among the rocks during both day and night. Although this predator finds fishes its chief diurnal prey, after dark it concentrates on crustaceans. In this region, as elsewhere, all nocturnal species are strictly predators.

Nocturnal activity in fishes over the open sandy bottom offshore largely involves the diurnally schooling fishes, discussed above, that migrate into that area after dark.

Diurnal predators feeding largely on fishes

Most diurnal predators feeding largely on fishes stalk their prey among the rocks, as does *Fistularia petimba*, or rush suddenly from cover to capture prey that have ventured near, as does *Epinephelus labriformis*. This is understandable, as their prey are mostly small fishes, such as pomacentrids and blennies, scattered among the rocks. Being so close to the substrate, these prey-fishes would simply dive under cover before a straightforward open charge, like that of roosterfish and toros. Predators using the stalking or ambush techniques attain a position close to their prey before making an abrupt move forward for the capture. Thus their mode of hunting reflects the proximity of cover to their small prey.

Many predators considered here are variably active day and night. *Epinephelus labriformis*, as noted above, though largely piscivorous during the day, takes mostly crustaceans at night. Predators feeding largely on small fishes among the rocks during the day have more in common with some of the nocturnal forms considered above, such as *Rypticus bicolor* and *Alphestes multiguttatus*, than with most of the other diurnal predators considered in the next section. That diurnal activity in these predators is largely piscivorous, while similar activity after dark largely yields crustaceans, may be an expression of the fact that most small fishes diurnally preyed on by these predators are inactive under cover at night, whereas the reverse is true for most small crustaceans.

Diurnal predators feeding largely on benthic invertebrates

Most of the strictly diurnal predators active close to the bottom are included here, some of which tend toward omnivorous and herbivorous habits. Just as feeding habits in nocturnal predators reflect the activity of small invertebrates after dark, feeding habits in many diurnal predators express the relative inaccessibility of these small prey organisms in their inactive positions during the day. The shift toward a relatively greater consumption of various sessile organisms during daylight also suggests that immobile material may be relatively difficult to obtain at night, when movement is perhaps important for discerning food.

Capture of concealed prey.—The effectiveness of measures taken by small organisms in concealing themselves amid algae-covered rocks and under the sand during the day is expressed in the techniques used by various diurnal predators to capture them. Examples include a number of species' capitalizing on the fact that hidden prey are frequently driven from cover when the habitat is disturbed. Thus *Halichoeres nicholsi* and *H. dispilus* follow *Mulloidichthys dentatus* to snatch prey driven into the open as the goatfish gropes in the sand for food detected by its barbels. Similarly, a small *Mycteroperca rosacea*, which is largely piscivorous, and thus falls in with the predators discussed above, follows *Bodianus diplotaenia* for this same reason, feeding on small animals chased from cover as the labrid roots about among the rocks. On other occasions, *B. diplotaenia* itself follows the large parrotfish *Scarus perrico* to capture prey driven out of hiding as the powerful jaws of the herbivore scrape algae from the rocks. Longley (1927) described how the trunkfish *Lactophrys triqueter*, at Tortugas, utilizes a jet of water from its mouth to uncover small organisms buried in the sand, and how smaller fishes such as *Halichoeres bivittatus* follow closely to share in the exposed food. *Sufflamen verres* in the Gulf of California also exposes animals buried in the sand by uncovering them with a jet of water from the mouth, and on other occasions sweeps sand away from buried organisms with currents that it generates with undulating movements of dorsal and anal fins (Hobson, 1965a). Starck and Davis (1966) also remarked that nocturnally active invertebrates are largely unavailable to diurnal predators, except to those that have developed special means of getting at them. These authors cited the habits of *Dasyatis americana* and *Pseudupeneus maculatus* in excavating buried prey.

At least one diurnal predator, *Gnathanodon speciosus*, seems to have developed means of ready access to hidden organisms. In its unique manner of feeding, this jack does not seem required to seek out individual prey. Using its highly protrusible jaws, it moves rapidly through the algae growth on rocks, sweeping up hidden crustaceans and other small organisms, including small benthic fishes, in large numbers.

Algae as food.—Diurnal fishes that feed on benthic invertebrates from rocky bottom frequently ingest algae along with their prey. Often the plants seem to be taken incidentally, and not utilized as food. Nevertheless, many fishes that feed in this manner belong to groups with members tending toward omnivorous and herbivorous habits. Such species occur among the balistids, chaetodontids, and pomacentrids. Hiatt and Strasburg (1960) reported that the more advanced and highly specialized fishes on Marshall Island reefs appear to be those "heading morphologically and physiologically toward the lower trophic levels," that is, toward utilizing plants as food. In my earlier report (Hobson, 1965a), I noted that diurnal habits are the rule for herbivorous and omnivorous species. Starck and Davis (1966) also reported this to be true among reef fishes in the Florida Keys.

The cleaning habit.—Many of these same groups, especially the chaetodontids, pomacentrids, and labrids, include members that have specialized to varying degrees in adopting cleaning habits. Most of the relatively small-mouthed fishes that characteristically pick minute organisms from the surfaces of rock and coral engage in some cleaning of other species at one time or another. Most of this activity is incidental and as such contributes little to the total diet. In some species, like *Thalassoma lucasanum*, cleaning habits are most evident in juveniles; in others, like *Bodianus diplotaenia*, cleaning is limited to the juveniles. A few forms, such as *Heniochus nigrirostris*, are specialized cleaners as adults, and much of the regular activity in members of these species reflects this habit. I observed no evidence of cleaning activity after dark.

VULNERABILITY OF PREY UNDER STRESS

The stimulus situation created by a fish in distress elicits attack in a wide range of predators. Some species, like *Gymnothorax castaneus*, seem particularly sensitive to these stimuli. When, as described above, the scorpionfish darting from my path was attacked by a moray, the eel may have been responding to the flight of the scorpionfish, even though this prey was fleeing from me. Animals fleeing from a threatening situation, as well as those exhibiting unusual or erratic behavior, may be especialy vulnerable. On several occasions such individuals were noted to draw attack from predators that had otherwise been showing no sign of activity.

Once, a scorpionfish was predator rather than prey, as it darted up after (but failed to capture) a fleeing small *Alphestes multiguttatus* immediately after I had missed hitting the little serranid with my spear. Similarly a small *Mycteroperca rosacea* fled to the base of a large rock after narrowly escaping my spear, only to be immediately pounced on by a small octopus. Sharks have been widely reported (for example by Eibl-Eibesfeldt and Hass, 1959; and Hobson, 1963a) to attack a fish instantly and vigorously when they had peacefully coexisted moments before, the moment the fish has been hooked on a line and is struggling. Damselfish *Abudefduf troschelii* were described above attacking pearlfish *Encheliophis jordani* after the commensals had been removed from holothurians at the water's surface and were swimming toward the bottom. These pearlfish are specialized for life within holothurians, and in addition to an extremely elongated, attenuated body, they lack pectoral fins. When locomoting rapidly, they swim with an exaggerated anguilliform motion, and this unusual swimming motion may have attracted the attention of the damselfish.

CONCLUSIONS

1. In Bahia de Palmas many species of fishes form large, relatively inactive schools close to shore during the day. Included here are *Harengula thrissina*, *Selar crumenophthalmus*, *Caranx marginatus* (juvenile), *Selene brevoorti*, *Haemulon sexfasciatum*, *Orthostoechus maculicauda*, *Xenichthys xanti*, *Lutjanus argentiventris*, *Umbrina xanti*, and *Mulloidichthys dentatus*. All feed nocturnally on prey becoming available after dark.

2. Although some of these diurnally schooling fishes remain to forage at night in the vicinity of the diurnal schooling sites, most migrate varying distances offshore after dark. The former are largely bottom feeders and include *Haemulon sexfasciatum*, *Anisotremus interruptus*, *Lutjanus argentiventris*, *Umbrina xanti*, and *Mulloidichthys dentatus;* the latter feed mostly in midwater and include *Harengula thrissina*, *Selar crumenopthalmus*, *Lythrulon flaviguttatum*, *Microlepidotus inornatus*, *Orthostoechus maculicauda*, and *Xenichthys xanti*.

3. Most of the diurnally schooling fishes that prey largely on benthic organisms among the rocks at night also feed to a variable though lesser extent in these same areas during the day. Generally this diurnal activity does not involve members of the large schools, but rather fish swimming in small groups or as individuals. On the other hand, the diurnally schooling fishes that move offshore at night to feed largely in midwater do not feed during the day, but rather remain inactive in their large schools.

4. The large, dense schools which these nocturnally feeding fishes form during the day are incompatible with their activity after dark, and generally are abandoned at nightfall in favor of more loosely spaced feeding aggregations and independent activity.

5. In Bahia de Palmas, the occurrence of many large, inactive schools of fishes inshore during the day is related to the proximity of suitable nocturnal feeding grounds over the open sandy expanses, and perhaps over the canyons, offshore. Indirectly, the presence of these feeding grounds strongly influences the presence in the area of large piscivores that depend heavily on the schooling fishes for food.

6. Most of the larger inshore piscivores, including *Elops affinis*, *Mycteroperca rosacea*, *Caranx hippos caninus*, and *Nematistius pectoralis*, are primarily crepuscular predators on the diurnally schooling, nocturnally active fishes.

7. The formation of schools during the day reduces the threat of predation on the schooling fishes. The relative effectiveness of the school in providing this protection fluctuates with changing conditions, and this fact strongly influences the behavior of predators that exploit members of these schools.

8. The effectiveness of the school in providing protection to its members generally is maximal during midday and minimal during twilight. This difference in relative vulnerability at different times of day profoundly affects the activity patterns of the large piscivores that prey on the schooling fishes.

9. At all times of day increased vulnerability of schooling fishes is often associated with disorientation in segments of the school or isolation of one or a few of its members.

10. Of theories that have been offered to explain the role of the school in reducing predation, the theory with which activity in fishes considered here is most consistent is that efficient hunting requires most predators to direct their strikes at individual prey, and that such attackers experience difficulty when confronted by the many alternate targets presented by the school.

11. Schooling by some predators facilitates capture of prey.

12. The nocturnally active fishes are all predators. Most feed on small motile invertebrates, largely crustaceans, that become available after dark when the invertebrates themselves are active in exposed positions.

13. Although the open sandy expanses offshore are largely devoid of fishes during the day, these areas are centers of nocturnal activity. The vast majority of fishes active here at night are among those that school inshore during the day. The exodus of fishes out over the sand at nightfall coincides with the appearance here of nocturnal invertebrates.

14. Among the fishes, there is far less activity over inshore rocky areas at night than during the day. Aside from some of the diurnally schooling species mentioned above, nocturnal fishes foraging close to the rocky bottom after dark are mostly small, solitary predators that are relatively inactive under rocky cover during the day. They include *Holocentrus suborbitalis*, *Alphestes multiguttatus*, *Rypticus bicolor*, and *Pareques viola*.

15. During the day the invertebrate prey of nocturnally active fishes are mostly under cover or otherwise unavailable as prey, except to those predators that possess specialized means of seeking them out.

16. Feeding habits among diurnal fishes are much more varied than those among fishes foraging at night. Many specialized feeding habits, such as the variable utilization of algae as food, and also "cleaning" habits, appear only among the predominantly diurnal species.

17. Smaller fishes feeding away from cover tend to aggregate. These groupings are most evident in diurnal species, like *Chromis atrilobata* and *Abudefduf troschelii*. Although *Myripristis leiognathus*, *Apogon retrosella*, and other fishes that feed in midwater at night also aggregate, their nocturnal groups are not so well defined and are more variable in form. Whether or not one regards these aggregations as schools, they probably function in much the same manner as do schools in reducing predation.

18. Most diurnal piscivores stalk their prey, as does *Fistularia petimba*, or rush out from cover, as does *Epinephelus labriformis*. Many with these habits are also variably active at night, when at least one, *E. labriformis*, preys largely on crustaceans.

19. Stimuli emanating from or suggesting injured and/or distressed prey elicit attack in a wide range of predators. Some species, such as *Gymnothorax castaneus*, are especially sensitive to such stimuli.

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